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MARCH 1985

THE BEHAVIOR OF THE HAWAIIAN SPINNER DOLPHIN, *Stenella longirostris*

By

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Melany Würsig, Shannon M. Brownlee,
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ADMINISTRATIVE REPORT LJ-85-06C

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The Behavior of the Hawaiian Spinner Dolphin,

Stenella longirostris

Kenneth S. Norris, Bernd Würsig, Randall S. Wells, Melany Würsig,
Shannon M. Brownlee, Christine Johnson and Jody Solow

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Santa Cruz, California

March 1985

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Administrative Report LJ-85-06C

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Figure 1. An adult male subgroup of Hawaiiin spinner dolphins interposed between the photographer and the school, Kealake'akua Bay, Hawaii. From a photograph by Randall Wells.

THE BEHAVIOR OF THE HAWAIIAN SPINNER DOLPHIN,
STENELLA LONGIROSTRIS

INTRODUCTION

This study of Hawaiian spinner dolphin behavior is based on several means of observation. Even in the calm lee waters of the Island of Hawaii wild dolphins are generally hard to observe and most encounters are brief. We hoped that data derived from divergent methods would in aggregate sketch in a more complete picture of dolphin life than we could obtain from any single method.

We observed and tracked them from shore stations, flew over their schools, radiotracked them, observed and photographed them underwater, recorded their sounds, swam with them, and photographed them from the surface at every opportunity. We visited a small captive school regularly to watch for details that were too fleeting at sea to be understood, and we tracked their reproductive physiology by taking and analyzing blood samples.

From all these less-than-comprehensive viewpoints a reasonably coherent picture of spinner dolphin life began to emerge. It outlines broadly what spinner dolphins do with their days. It only begins to tell us such finer details as how they signal one another, how their young are nurtured, how they deal with food and predators, and what interdolphin relations consist of.

The large evolutionary questions centered around their social structure are only incompletely answered. We did find remarkable fluidity of school composition and of association patterns within their schools. But we also found some associations between pairs of dolphins lasting as long as our study. What the balance between kin-related phenomena and the non-familial aspects of spinner dolphin society is cannot be stated with any precision though we are clearly dealing with schools that shift radically from day to day in composition, even including most individual associations.

This study, so far as we are aware, is the first to make extensive underwater observations of wild dolphins. This work allows a first analysis of signal systems and association patterns between such wild dolphins.

Drawing from all these lines of inquiry, we have evolved a series of working hypotheses about how various aspects of dolphin societies function. These views, we think, are important grist for future debate so we present them here in a series of paragraphs entitled: "Interpretations."

Our subject, the Hawaiian spinner dolphin (Figure 1), is closely allied to other Pacific spinner dolphins, differing only in minor characters of proportion, associated measurements, skeletal details and color pattern. It appears most closely allied to the whitebelly spinner of the offshore eastern tropical Pacific, from which it differs modestly in pattern and size (Per-rin 1972).

Unlike the oceanic spinner dolphins, the Hawaiian form typically comes close to the shores of volcanic islands and atolls during the day, instead of spending its entire life in the open sea. This unusual habit allows exceptional access to the form for study. And while many of its schools frequent rough waters open to the sea, some occur in the lees of islands and even inside atoll lagoons where they may be observed in clear, calm water. The best such situation known to us occurs at our study area in the lee or Kona Coast of the Island of Hawaii. There a half-circle shaped area of calm water usually extends along the island coast from about Mahukona on the north to Milolii on the south, a distance of 100 km. The water usually grades from glassy calm in the morning near shore, outward into increasingly oceanic seas until the lee is gone altogether about 10 km offshore (Figures 2,3).

This work builds upon an earlier reconnaissance study of this population of dolphins (Norris and Dohl 1980). That earlier work outlined the daily behavioral cycle and began the process of understanding school structure. Our task here was to check and refine the conclusions of the earlier study, to approach questions that it posed, and to extend the analysis using newer or more precise methods.

The specific research objectives of this study are these:

1. To outline the structure and composition of spinner dolphin schools through time, and to define the ways in which such schools support such crucial activities as reproduction, nurture and feeding.

2. To define the acoustic correlates of different behavioral states, and to search for context-specific uses of such sounds.

3. To define the leadership or "decision making" processes of spinner dolphin schools, and more specifically to assess whether or not certain individuals were crucial to school function, especially in carrying out learned functions of a school, such as location of specific rest sites along the Hawaiian coast.

4. To define the composition of schools and of their various subgroups, including age and sex groupings within schools, and the determinants of school numbers.

5. To determine gross reproductive rates from an estimation of the total population combined with data derived from the numbers of calves, juveniles and adults sighted.

6. To study the interactions of parts of schools.

7. Using a comprehensive photographic scars-and-marks catalogue, to identify as many individuals, their movements and interactions as possible.

8. To study in a refined way the movement patterns and changes in diving patterns of spinner schools in daytime near the shore, using theodolite tracking.

9. To study similar movements offshore, along other sections of coastline, and at night by means of radiotracking.

10. To define the gross movements, distribution and population size of dolphins clustered around the Island of Hawaii. This information is needed to understand the broader question of what use spinner dolphins make of islands within their overall geographic range.

11. To work underwater with dolphin schools using observation, listening and photography to begin the understanding of interdolphin relations within a school.

12. By the same means to begin definition of the system of signs and signals used by spinner dolphins.

13. To begin definition of the geometry of spinner dolphin schools and its determinants, and especially to move toward understanding of what we call "the sensory integration function" of dolphin schools.

14. To define certain aspects of locomotion and respiration using underwater observation and photography.

15. To define the physiological correlates of reproduction by analysis of hormone levels in captive animals.

16. To add to knowledge of the feeding habits of spinner dolphins.

We hoped that the results of our work on these island-associated dolphins could be applied to understanding oceanic populations associated with the yellowfin tuna industry. In retrospect we feel that in general it probably can. It is becoming clear that association with islands by spinner dolphins is behavior that occurs widely throughout the tropical ocean wherever islands occur within their range. And while many identified animals remain near the shore of the Island of Hawaii throughout our study, our population seemed "open ended" in that the rate at

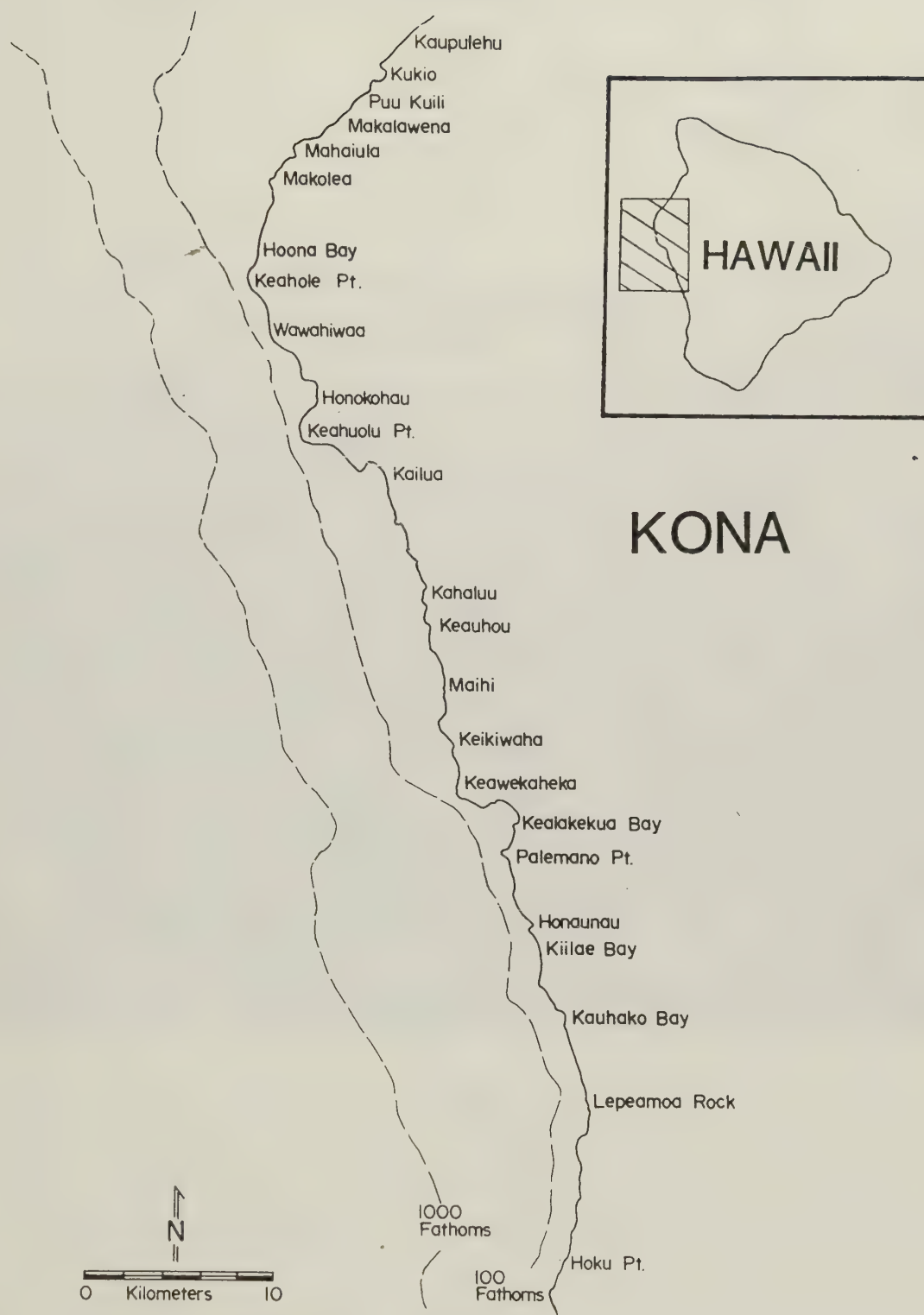


Figure 2. The Island of Hawaii and detail of the Kona Coast.

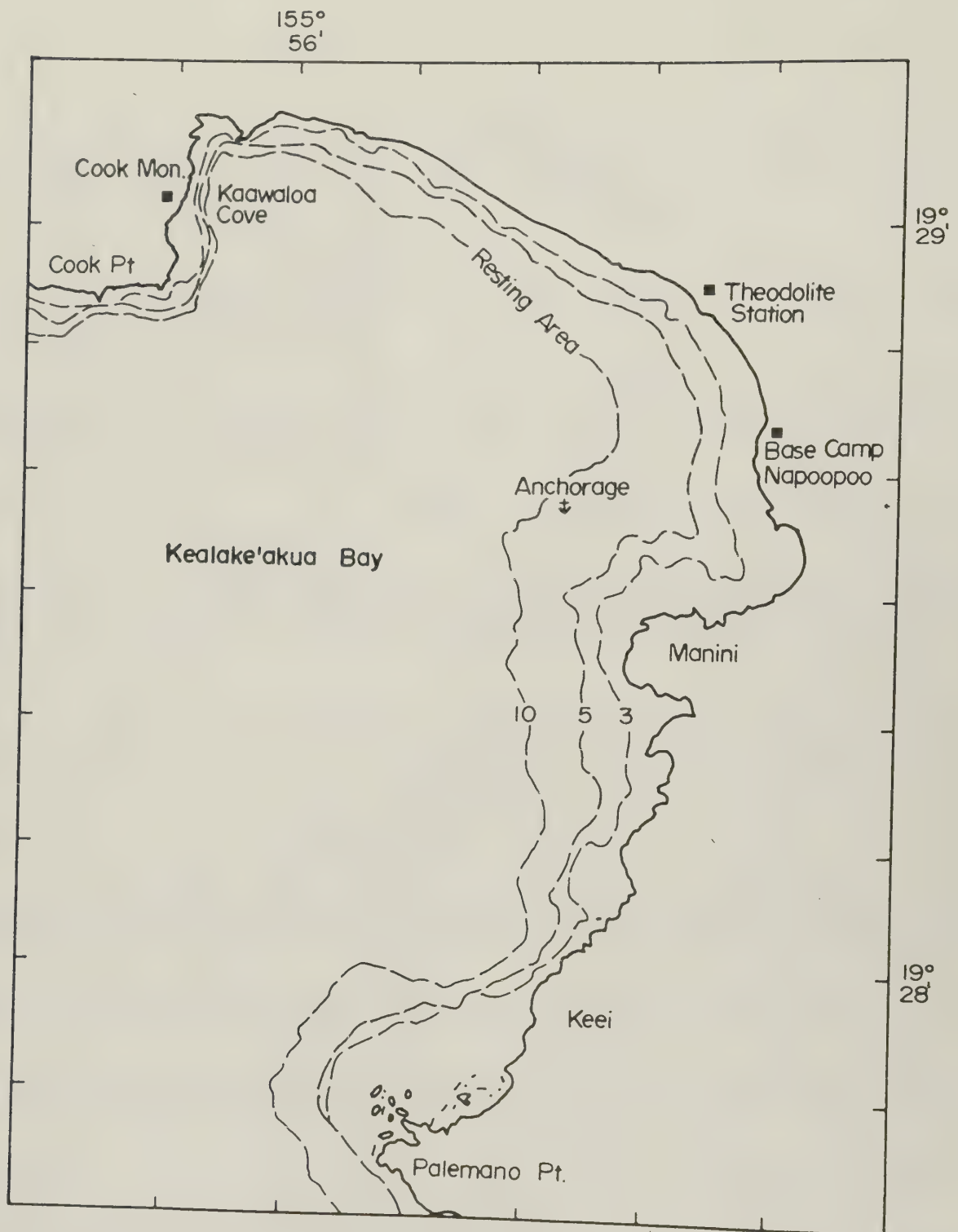


Figure 3. Kealake'akua Bay, showing geographic names and locations of shore bases. "Resting Area" refers to the general location where dolphins spent most of the day.



Figure 4. Kealake'akua Bay from the air. Base camp is in the lower left. Cook Monument is top center.

which new animals were recruited into our marked population never leveled off throughout our work. Once the initial flush of identification was past new animals appeared at a quite constant rate until completion of our study as if they came in from a larger, probably offshore population.

We expect, but cannot prove that wherever islands exist in the open tropical Pacific, and probably beyond, they will be used by these dolphins for rest periods, feeding and probably reproduction. Where islands do not exist the animals somehow do without them or do not occur. We will discuss this point later in the paper.

At the close of this paper we propose a model for the tuna-dolphin relationship that draws from several aspects of this study, and from knowledge of dolphins and tunas derived from fishery studies. We recognize that this is an "interpretation" but it is a broadly based interpretation that, if correct, could have importance in fishery management.

The data base developed by this study is considerable. For example, about 20,000 photographs were involved in our scars-and-marks catalogue, allowing us to identify reliably 192 individual dolphins. Observation time from our various vantage points of aircraft, theodolite station, viewing vehicle and by swimmers was extensive, and is outlined under materials and methods.

But as is probably true in any complex study, at the end we wished for more complete records of certain kinds. Especially we wished for more photographic sequences underwater, and better correlation between emitted sounds and animals under observation. The opportunity opened by frame-by-frame analysis of underwater behavioral events was only just begun by this program.

We describe our techniques and equipment in detail in the following section. Following that we present the results of the various subprograms, and then in the discussion, attempt to bring these results together into a synthetic view and to compare it to the findings of other studies of dolphin behavior. We attempt to frame these findings more broadly too, in terms of knowledge of other higher mammalian societies. And finally we try to reflect these findings and interpretations back on the problems of dolphin interaction in the yellowfin tuna fishery.

MATERIALS AND METHODS

Base Camp and Research Party

A base camp was established in a rented waterfront house in the village of Napoopoo, on the south limb of Kealake'akua Bay. This house allowed us easy access to our two boats moored

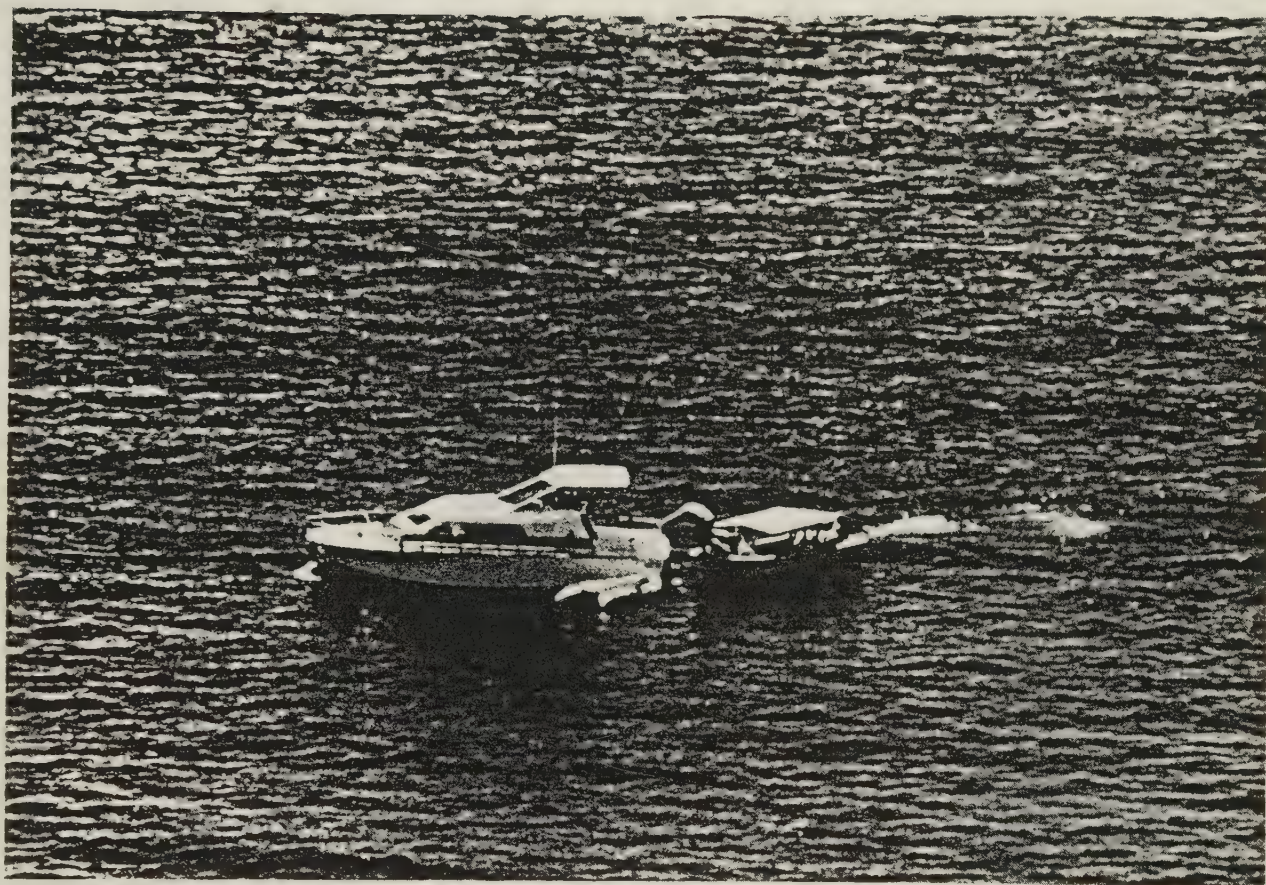


Figure 5. The cabin cruiser Nai'a, with the underwater viewing vehicle Maka Ala astern.

offshore, and provided a panoramic view of the bay for monitoring school movements. Radio contact was established by VHF Radio both to the theodolite tracking station on a nearby cliff, and to vessels working offshore (Figures 3, 4 and 5).

The scientific party, which varied in number, but was usually about six people, was housed at Base Camp. A fair proportion of the routine part of the study was carried out by volunteers. The full time members were chosen for a variety of skills needed in such a broad program, and while all contributed to every part of the program there were general assignments for each. These were:

Dr. Kenneth S. Norris	Principal investigator
Dr. Bernd Würsig	Field camp supervisor, behavior, photography, theodolite and radio tracking, animal capture, electronics, and statistical analysis.
Mr. Randall Wells	Boat operations, flights, hormonal studies, photography, oceanarium observations, tagging and radio-tracking.
Ms. Melany Würsig	Theodolite tracking, photography, daily scans, statistics, and data reduction.
Ms. Christine Johnson	Maka Ala observations, underwater photography interpretation.
Ms. Shannon Brownlee	Acoustic recording and analysis, graphics.
Ms. Jody Solow	Free swimming observations.

A separate camp was established at Makalawena Beach, about 45 km north of Kealake'akua Bay, because free-swimming studies were disrupted by vessel and other activity common in Kealake'akua Bay. This camp allowed us to sample two rather distant points within the Kona population simultaneously. The Makalawena site is adjacent to the shallow water sand flats that accommodate the largest inshore schools of spinner dolphins along the entire Kona coast.

Flights

Twenty-three complete circuits of the coast of the Big Island (The Island of Hawaii) were conducted using a small plane usually on a biweekly basis from August 22, 1979 to August 31, 1980. Planes used were either a low-winged Piper Cherokee, or a Cessna 172. The crew on these flights consisted of a pilot and a

primary observer/photographer in the front seats, and one or two secondary observers in the rear seats. Surveys were flown at 150m altitude at a velocity of 170 km/hr, and at a distance of about 0.5-1.0 km from shore. Flight paths were flown alternately clockwise and counterclockwise to standardize for the tendency of spinner dolphins to move offshore in the afternoon, so that particular areas were not consistently surveyed in the morning and others in the afternoon.

Three additional flights were dedicated to examining the structure of dolphin schools and the movements of specific schools along the Kona coast. These flights, on August 2, 1980, August 16, 1980, and September 7, 1980, involved repeated observations of selected dolphin schools during the 10+ usable hours of daylight.

All sightings of marine mammals were recorded. Some schools were circled for as long as 45 minutes. During these circles the species was identified, school size was estimated, school structure and activity were described, associated organisms and boat activity were noted, environmental factors such as surface conditions, distance from shore, characteristics of the coastline, and the presence or absence of a visible sea floor beneath the animals were recorded. Photographs were taken for school size estimates, and for studies of composition and geometry. In Kealahou Bay, simultaneous group size estimates were sometimes made from aircraft, shore, and boats for later comparisons with photographic records.

The regularly recorded sighting factors of greatest influence included sea height and degree of whitecapping, underwater light penetration as affected by sun angle, glare, cloud reflection, rain, turbidity and turbulence. The most common conditions during each three-month season are depicted on sighting maps (Figures 7-11) and are categorized as follows:

- (1) Excellent -- 10% whitecaps or less, little or no glare inshore of the plane (where most spinner dolphins are seen), good light penetration, and the absence of chop that might obscure dorsal fins at the surface;
- (2) Good -- up to 20% whitecaps, some glare and little chop;
- (3) Fair -- 15-30% whitecaps, chop or heavy seas, glare, but still a reasonable chance of sighting dolphins;
- (4) Poor -- over 30% whitecaps, glare, poor light penetration and/or rain squalls, heavy turbulence, with little chance of sighting dolphins.

The aerial surveys were designed to provide both census data and to study the group structure and behavior of dolphin schools during morning and early afternoon when spinner dolphins were

typically near shore, and when sighting conditions were best. Unavoidable non-uniform sighting conditions around the island doubtless introduced bias into our counts, favoring the calm parts of the island shore. Nonetheless we feel they provide a reasonable indication of total population size, and should be regarded as minimum estimates.

Daily Scans

From May 1979 through May 1980 a twice-hourly log of dolphin activity within Kealake'akua Bay was kept. During the first two months of observation these scans were recorded from Manini Point, at the southern edge of the bay, and later from a cement platform 5 m above the mean low water, at Base Camp. Some scan data were obtained from the higher vantage point of the theodolite station. Concurrent data from both sites showed that the information from each was comparable despite the difference in viewing angle.

The observation protocol was as follows. Beginning at the first half hour of light and for every half hour until and including 1800 (earlier during winter) an observer recorded weather information (cloud cover, wind, sea state), the number and activity of boats in the bay, and any miscellaneous information the observer felt was of importance. The bay was scanned for dolphins with 7X binoculars. If no dolphins were seen the scan lasted 10 minutes, to make certain that diving animals were not missed. If dolphins were sighted then the group size and general activity level (traveling, resting, socializing etc.) were assessed and all aerial activity was counted for a five minute interval. We also estimated the position of schools. These data are only rough estimates. Precise records of position relied upon theodolite tracks. Good consistency in estimates of group size, counts of aerial activity and assignment of general behavioral category was, we believe, achieved between observers.

Data on group size and aerial activity were subjected to computer analysis deriving the amount of activity per animal per hour of the day (Figures 14-17). Because we were almost always aware of when animals entered or left the bay we were able to obtain information on the frequency of aerial activity, amount of time spent in the bay by season and group size.

The scans tended to pick up schools after they had entered the mouth of the bay and were some distance inside. Hence the descent into rest had probably begun before or during our first sightings and these early morning records should not be taken as indicative of activity levels of schools at sea.

Although the daily scans tended to restrict at least one member of our crew to camp for two or three hours before they were relieved, they allowed us to gain the information mentioned above, but perhaps more important, they ultimately gave us an

almost intuitive feel for how spinner dolphins spent their days near shore. For example, we became aware that our own observation activity on boats disturbed the dolphins early in their entry into the bay, while later on they were less disturbed. The animals seemed to "settle in". We were able to coordinate our activities accordingly.

Theodolite Tracking

For precise tracking of dolphin schools in Kealake'akua Bay an observation platform was established 72m above mean low water up the very steep slope at the back of the bay. By means of a Nikon Model NT-2A theodolite (or high accuracy surveyor's transit) we obtained azimuths and dip angles from the station to the dolphin school. These readings, along with behavioral observations, were spoken into a cassette tape recorder and later transcribed into data logs.

The readings were converted to x and y coordinates on a map of the area by use of a computer program utilizing an iterative correction for the curvature of the earth (developed by J. Wolitzky, and described in Würsig 1978).

The theodolite tracking technique, developed by Roger Payne of the World Wildlife Fund, allows accurate tracking of marine mammals from onshore observation sites. Here, the accuracy of the theodolite (= 10 seconds of arc) and its placement 72 m above mean low water allowed determination of a dolphin's position within approximately ± 10 m at 3 km distance. Our records were plotted on a bathymetric chart which we constructed at Kealake'akua Bay. Dolphin speed and direction assumes a straight line path between readings, because not every shift in direction made by dolphins was recorded. Speed readings were analyzed only if they were made within 10 minutes of each other, in order to minimize errors due to change of direction.

Bottom type was plotted on our bathymetric chart to relate using a fathometer on our survey vessel, Nai'a, visual sightings of bottom type from the viewing vessel Maka Ala, and a concurrent plot of ship position using the theodolite. This record was imperfect at deeper than about 10 m because poor visibility caused uncertainty about classifying bottom type.

Movement patterns of dolphin schools relative to boats were obtained by concurrent tracking from the theodolite station. This allowed us to assess the effect of such vessels on dolphin movements.

Scars and Marks Catalogue

Although to the casual observer, individual dolphins appear much alike, many animals exhibit pigmentation patterns and scars

and marks that allow individual recognition. Especially the trailing edge of the dorsal fin, which is thin and easily tattooed, is often different enough to distinguish individual dolphins (Würsig and Würsig 1977, 1979; Shane 1980; Wells, Irvine and Scott 1980; all for the bottlenose dolphin, Tursiops truncatus). The smaller, more pelagic dolphins in general have fewer marks than coastal bottlenose dolphins, but Norris and Dohl (1980) showed that similar work could be done with spinner dolphins.

Each time a school of spinner dolphins was encountered a suite of photographs was taken of as many individuals as possible, and of the various subgroups within the school. We used mainly Pentax MX 35mm cameras with powerwinders and Kodachrome 64 ASA film. Lens sizes ranged from 50-300mm, with 200mm the most commonly used lens from our small boats. Frame numbers were recorded for each suite of photographs, and the location, and relevant observations of behavior were also recorded in a film log.

Records of nicks and cuts in the posterior margin of the dorsal fin proved especially useful because such marks could be rephotographed frequently, and usually from either side. Deformed or folded fins were recorded. Scars or special pattern marks on the body were also recorded but were less useful because they were infrequently seen. Slides of animals bearing scars and marks were projected and distinctive fins were traced, resulting in a catalogue of individuals, dates and places of occurrence, and associates.

Least useful in this study, but also recorded, were marks that could be seen only below the surface. These were recorded visually from the viewing vehicle, by Eumig Nautica Super 8mm underwater cine' camera, and by 35mm camera from inside the viewing vehicle. Because our underwater work was confined to only two locations, such marks did not often tell us much about movements of individuals, and repeat observations of the same animal on different days were infrequent. Nevertheless, these marks proved useful during single observation sessions. In a longer term underwater study they would probably prove more widely useful.

A matrix of sightings, resightings and associations was developed. From this data base interpretations about individual movements, association patterns and times of sighting were derived. Because only a proportion of animals in a school (about 20% or less) could be identified by photography, our interpretation depend wholly upon those animals whose identification we felt was secure. The absence of any particular individual in the photo record is not proof of its absence from any group, because photo opportunities for some schools were limited and all animals were not always photographed.

Dolphins that were sighted five or more times during our one and a half year stay were subjected to analysis of frequency and location. A matrix of occurrence in different areas along the Kona coast of the Island of Hawaii was developed by Donald Croll and run on a Hewlett Packard 9845 computer and plotter at the Moss Landing Marine Laboratories, Moss Landing, California.

Tagging and Radiotracking

Four spinner dolphins were tagged during this study (Table 1). Bow-riding dolphins were captured with the tail grab device designed by Dr.'s Roger Payne and Bernd Würsig, and used successfully with dusky dolphins (Würsig 1976). As the grab makes contact with the animal, a trigger is released that allows a padded grab to clamp around the peduncle, and the grab separates from its long handle. The dolphin is retrieved with an elastic shock cord and nylon line attached to the grab. In our study it was then lifted carefully into a 2.7 m inflatable boat alongside the capture boat. While one person on the capture boat monitored respiration and general condition of the dolphin, two others in the raft measured and sexed it, drew blood samples from the flukes (two dolphins), marked the dolphin and released it. One animal was freeze-branded using a 7.6 cm metal numeral brand, supercooled in liquid nitrogen and applied to both sides of the dorsal fin for 15 seconds. Small (less than 2 cm deep) notches were cut in the trailing edges of the dorsal fins of two dolphins. Colored roto tags (Nasco, Inc.) were attached to the dorsal fins of three animals.

Radio transmitters (Telonics, Mesa, AZ, models MK-II, and MK-V-4A) transmitting at 148+ MHz, were placed on the dorsal fins of the three animals. A 47.0 cm stainless steel wire antenna was attached to the back of the transmitter. The transmitter was fastened to a padded backing plate which was through-bolted on spring-loaded bolts with dissolving nuts to two padded washers on the other side of the fin. The first transmitter was designed to release within 48 hours, while the next two were supposed to remain for approximately three months. Transmitters operated continuously.

Signals were transmitted at a rate of once per 0.9 seconds. Following tagging, the animal was photographed and released. The entire process from capture to release took 10 - 30 minutes depending upon the number of procedures performed.

Tracking was accomplished in several ways. Modified Automatic Direction Finders (ADF, Ocean Applied Research, Inc., San Diego, California) connected to Adcock antennas were mounted on the vessel Nai'a, and also used from a vehicle on shore. Signals received by the ADF's were presented visually as a flashing bearing relative to the bow of the vessel. An audio signal accompanied each flash, and the intensity of the signal was shown on a meter as an indication of distance from the transmitter.

Table 1 . Hawaiian spinner dolphin tagging summary.

<u>Date</u>	<u>Tags</u>	<u>Location</u>	<u>Group Size</u>	<u>Sex</u>	<u>Measurements(cm*)</u>			<u>Comments</u>
					<u>1</u>	<u>2</u>	<u>3</u>	
Sept. 28, 1979	Freezebrand #1 Rototag, yellow #5 V-notch, midfin	Keahole Point	150	Male	170	28.3	71.5	Resighted twice: 1) Reported from Mahukona, Nov. 1, 1979. 2) Seen in Kealake'akua Bay, Nov. 14, 1979. Marks visible each time.
Oct. 25, 1979	Radiotag #1(RT-1)	Wawahiwa Point	100	Female	183	34.0	85.0	Tracked from 10:05 until 15:40 on Oct. 26, when the signal was lost. The package was loose on the fin in photos near the end of tracking.
Nov. 01, 1979	Radiotag #2(RT-2)	Hoona Bay	30-40	Female	177	34.5	79.5	Tracked until morning of Nov. 6, when signal became weak and was lost. Seen in Kealake'akua Bay on Nov. 14; 1 of 2 mounting bolts was missing, but rototag was intact.
April 26, 1980	Radiotag #3(RT-3)	Kahaluu	30	Male	172.5	NA	NA	Tracked from 10:44 until 18:30 on Apr. 27, when the signal was lost after becoming weak and irregular. Resight- ed in Kealake'akua Bay; 1) Apr. 28, antenna missing. 2) Apr. 29. 3) Apr. 30. 4) May 01. RT-3 was consistently in groups of 30-100. It appeared healthy, and the package seemed intact and well-mounted, except for the broken antenna.

*1= tip of rostrum to fluke notch; 2= tip of rostrum to center of eye;
3= tip of rostrum to leading edge of dorsal fin. All measurements are
straight-line.

Attempts were made to stay within approximately 1 km of the radio-tagged dolphins. Transmitter range varied from less than one kilometer to several kilometers depending upon individual transmitter and sea state. The mobile shore station operating from variable heights up to 450 m, had significantly better reception than the shipboard receiver. The shore station helped in triangulating positions at night. Positions, depth, and environmental conditions were plotted approximately every hour.

Surfacing times were recorded manually every four hours and continuously using a Rustrak chart recorder. During daylight the school containing the radiotagged animal was approached hourly to observe behavior, note school size, describe shape and dimensions of the school, record the interactions of the tagged animal and others in the school, and photograph identifiable animals in the school.

Offshore Studies

Our 7.6 m Skipjack inboard outdrive vessel Nai'a, equipped with twin OMC 140 HP gasoline engines, supported offshore work outside the confines of Kealake'akua Bay. The ship was equipped with a single sideband radio, and a VHF radio system including handheld portable stations. A Furuno Model FE500 Recording Depth Finder, and an acoustic recording cabinet were mounted in the open cabin. A small inflatable life raft was aboard. The vessel had facilities for four workers, allowing us to cook and sleep on board for rather extended stays in sheltered waters, and it could operate to about 10 km offshore in the lee of the Island of Hawaii.

Acoustic Studies

Acoustic recordings were made on 34 days, for a total of seven hours of tape during the following eight recognizable sorts of behavior: (1) entering (animals coming to bays to rest), (2) descent into rest (schools in the process of changing from active patterns to quiescence), (3) rest (schools with slow locomotion, synchronous diving and suppression of active social patterns such as caressing), (4) zig zag swimming (a period following rest in which schools abruptly and repeatedly change course and swimming speed), (5) travel (a very active period in which schools move rapidly in concert), (6) spread formation (after traveling to sea, schools abruptly disperse), (7) feeding (near dusk and at night schools move in a single direction and dive subsynchronously), (8) socializing (some schools before and after rest may engage in intense caressing patterns), and (9) meeting (when two schools meet and either merge or separate again).

Recordings were made with a Lockheed 417 1/4 inch tape recorder at 15 inches per second. An H56 Naval USRD hydrophone attached to a 10 m coaxial cable was deployed with an elongate water-noise reducing float attached to the cable four meters

above the hydrophone. This equipment was calibrated once a year by the Navy Sound Reference Laboratory. This system was flat to 65 kHz, limited by the hydrophone.

All recordings were made from the Nai'a. When a school was located the boat was positioned ahead of the school, stopped, and the gear deployed off the stern. The hydrophone hung four meters below the surface. Schools recorded varied in size from seven to over 100 animals. Most recordings were done in the vicinity of Kealake'akua Bay, though we recorded as far north as Hoona Bay and as far south as Milolii.

Recordings and surface behavioral observations were all made when the animals were within approximately 300 m of the drifting boat.

Behavioral observations were of two kinds. First, the frequency and kind of aerial behavior (which is a general indicator of school activity), and the number of animals, their distance from the boat, their orientation to the recording gear, and recording conditions were spoken into a voice channel while recordings were being made. These observations allowed us to typify behavioral state and to calculate the relationship of signal abundance to animal numbers. We were also able to select portions of tapes when animals faced the recording gear, and were within good recording range.

Second, once every half hour a 10 minute scan was made for such information as the behavioral state of the dolphins, weather and sea conditions, swimming behavior such as synchrony of movement, speed, and the dimensions of the school. We also quantified aerial behavior and made an assessment of social patterns seen through the surface.

The original recordings were dubbed onto 1 inch tape and processed on an Ampex instrumentation recorder. By selection of the best recordings four of the original seven hours were dubbed. Recordings were excluded if: (a) the animals were 100 m or more away from the hydrophone or moving away from it, (b) the animals were generally facing away from the hydrophone or moving away from it, (c) the sound level was especially faint, (d) background noise, especially snapping shrimp was high enough to mask dolphin sounds.

Recordings were analyzed using the waterfall display of a Spectral Dynamics spectral analyzer. Tape was run a 1/4 speed (3 3/4 ips). The analyzer was set for 25 Hz resolution, 20 kHz range, linear display, and transform size of 2048. This meant that the output range was from 0-80 kHz, and the real resolution was 100 Hz.

From 18 to 32 samples were taken for each behavior class except Zigzag Swimming. The zigzag period was excluded from the

statistical analysis for reasons that will be discussed later. A total of 198 five-second long samples was printed on a Tektronix printer using photosensitive paper, which produced a time/frequency plot. Each sample was examined for the number of whistles, clicks, and broadband burst pulse signals. The number of each signal type was divided by the estimated number of animals present in order to obtain the estimated number of sounds per animal for each sample. There are unavoidable uncertainties in this method having to do with accuracy in estimation of animal numbers, and the number of animals phonating toward the hydrophone. We are confident that the animal numbers estimate is generally accurate to within about 25%, based on other comparisons of numbers estimation. It is probably true that most of the time some animals while swimming underwater did not face our hydrophone, even though we judged the school to be moving toward it. Such an error is conservative, reducing the apparent correlation between animals and sounds per unit time. So where our figures show high correlation between a behavioral class and a given sound emission frequency, it is probably even higher by an unknown factor.

Underwater Observations

Three means of underwater study were used. First, direct observations were made from the viewing vessel Maka Ala. Second, underwater photography was employed, and third, direct observations were made by a swimmer.

The viewing vessel (called the Maka Ala, Hawaiian for "watchful one"), a modified Boston Whaler skiff, had a rectangular plexiglas chamber inset into its bottom at the bow end (Figure 5). The observer, lying on a mattress, spoke notes into a tape recorder and could photograph and listen to the animals simultaneously.

Since the plexiglas bow chamber had been built to conform to the vessel contours it allowed useful visibility downward, to the sides, and ahead, but not upward toward the surface. This proved to be a serious detriment because determining the sex of spinners underwater is usually done by looking upward at the animals from below, which we could not do.

Nonetheless means of determining sex of dolphins became simpler as the project wore on. At first, only direct genital examination could be used because of the very subtle dimorphism shown by the species. But, as our experience grew we became able to interpret fin shape (erect, tall triangular fins in old males), and especially details of the tail stock (in adult males a modest post-anal hump is present and the tail stock itself is notably thickened dorsoventrally). We learned to recognize groups of old males by these features and by their resolute swimming behavior and habit of interposing themselves between us and the remainder of the school (Pryor and Kang, 1978, and Figure 1).

A listening system was evolved for the Maka Ala that allowed us to hear animals in spite of both the outboard engine and the water noise of the moving vessel. This consisted of a Gould CH-17UT hydrophone mounted inside a waterfilled PVC plastic tube oriented foreward into the water stream. The hydrophone was partially shielded from the engine noise with a foam neoprene barrier. The system was mounted below the bow chamber. The observer could simultaneously listen through headphones and record. Visual observations and acoustic recordings could be keyed together on a two track recorder.

Most observations from the Maka Ala were made in Kealake'akua Bay because the seaworthiness of the vessel was suspect (rightly so, it turned out, when she sank in a very heavy rainstorm).

Underwater filming used an Eumig Nautica Super 8mm camera. Films were obtained both in the Maka Ala and directly by swimmer. The most successful method consisted of insinuating a swimmer into the schools from an outboard-powered inflatable boat. The photographer, situated under the bow, held the bow painter and with feet on an athwartships line going under the craft, rode into schools of dolphins on the slowly moving boat. Once in the school, the engine was idled or stopped and the swimmer moved quietly foreward, away from the gliding boat and toward the animals. By reloading from the quietly moving boat sometimes three or four 3 min. rolls of film were taken in a single episode. The animals were sometimes remarkably tolerant of the swimmer. Many films were made of dolphins swimming within a meter or so of the swimmer.

Usable films were later analyzed on a film editor (Elmo Editor Model 912) frame by frame. Knowing the filming frame rate (15 frames/second) we could time behavior patterns and social signals to within fractions of a second. These measurements are possibly subject to error from differing states of battery drain during photography. The frame rate was checked by photographing a stop watch.

Attempts to insinuate a swimmer into wild schools were carried out at first in Kealake'akua Bay and later off Makalawena Beach, where a camp was maintained from November 1979 to July 1980. Each morning, weather and the presence of dolphins permitting, the swimmer and a companion went to sea in an inflatable boat equipped with a 15 hp engine. The school was slowly approached and the swimmer entered the water equipped with a safety buoy, wet suit, and an underwater notepad. The swimmer emitted a mimic of a dolphin squeal at frequent intervals as an announcement to the animals, and then attempted to swim among them.

Observations of Captive Spinner Dolphins

Through the courtesy of Sea Life Park Oceanarium at Makapuu Point, Oahu, we were able to observe a school of captive spinner dolphins held in a roughly circular 27 m diameter pool, 5m deep (Bateson's Bay). These animals, scarred and not considered fit for public display, were undisturbed except for daily feeding periods and periodic medical attention.

These animals were:

- (1) Kahe - Female from Waianae Coast, Oahu, est. 11 yrs. old;
- (2) Lioele - Male from Maile Point, Oahu, est. 16 yrs. old;
- (3) Kehaulani - Female from 5 Needles, Lanai, est. 12 yrs. old.

The large pool was equipped with a capacious viewing room on the deepest side of the tank, with four viewing ports; two plastic hemispheric bubbles of 1.5 m diameter curved into the tank and two flat glass ports 1 m square (Figure 6). Cables for listening gear were run through the roof of the viewing room and hydrophones were suspended in the tank in front of an appropriate viewing port. Outside lights on the periphery of the pool could illuminate the tank at night. Because of other park lights the tank was never totally dark. It was supplied with fresh sea water at a high volume from a holding tank and water was drawn off into a central drain box, which usually created a modest vortex.

Observers talked commentary into a cassette tape recorder at the same time dolphin sounds were being recorded or listened to through headphones.

A series of behavioral observations of the captive school were made between September 1979 and October 1980, and in June 1981. A 24 hour observation session was made every two weeks. During this session observations were recorded for 10 minutes every half hour. Unscheduled observations that sometimes lasted a full 24 hour day were made of various aspects of behavior. The special behavior patterns studied were bout behavior, aerial behavior and its precursors, the dynamics of school leadership, echolocation "manners", acoustic intimidation, affiliative patterns, feeding, play and the use of sound in prey capture.

Reproductive Studies

Reproductive seasonality, behavior and physiology were examined in various ways. The percentage of calves in schools photographed from the air was determined. A calf was an animal equal to or less than 0.75 the size of the nearest large animal. The

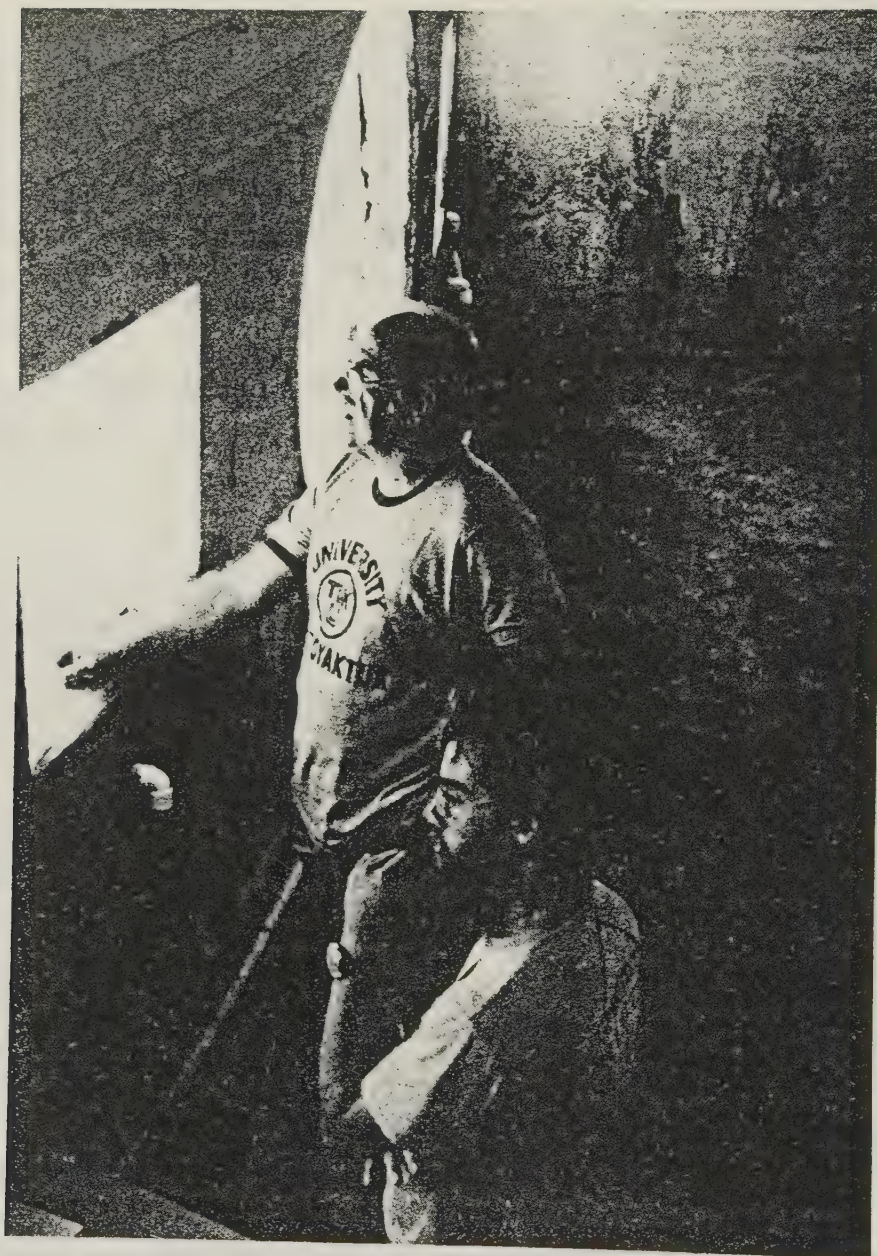


Figure 6. The underwater viewing room at Bateson's Bay, Sea Life Park oceanarium, Oahu, where our captive observations were made.

calves were required to maintain this proportion through a series of at least three photographs in order to score as a calf, as a control for various swimming attitudes relative to the airplane.

The dates of captive births (courtesy of Ingrid Kang, head trainer at Sea Life Park) were combined with age data on captives determined by tooth growth layer analysis (courtesy of Dr. A. Myrick of the U.S. National Marine Fisheries Service, La Jolla) to provide information on reproductive seasonality for 10 captive spinner dolphins.

Serum steroid hormone concentrations were measured every other week for 3-5 captive spinner dolphins at Sea Life Park, from September 1979 through October 1980, and again in June 1981. Serum was obtained from 24-36cc blood samples drawn from fluke vessels. Serum samples were then frozen for delivery to the analyzing laboratories.

Male serum was analyzed for concentrations of testosterone by radioimmunoassay technique (Smith-Kline Laboratory, Honolulu, Hawaii; sensitivity = 0.05 ng/ml). Similar methods were used to analyze female serum for estradiol (Smith-Kline Laboratory, Honolulu, Hawaii; sensitivity = 1.9 pg/ml) and progesterone (sensitivity = 33 pg/ml), through the courtesy of Vicky Kirby, San Diego Zoo Research Laboratory.

Behavior related to or indicative of seasonal reproductive state was recorded from the side of Bateson's Bay, at Sea Life Park. The following categories of behavior were recorded: (1) associations between individuals including duration, frequency, relative position and interactions, (2) individual patterns such as aerial behavior, (3) activity level, (4) respiration rates, (5) location and headings. One animal was considered to be associating with another if they swam or surfaced more or less synchronously, within about 2m or less of each other.

Terminology

Certain terms are used throughout this study with very specific intent. We define them as follows:

School: Any aggregation of aquatic animals that swim together as a unit (see Norris and Dohl 1980). This means that any group of dolphins we see traveling together for long enough to make us sure they represent a cohesive unit we call a school. Schools have ranged from groups of four animals to ones of about 225 animals in this work. If a large school is harrassed it may fragment into two or more smaller groups that we then call schools if they move off separately and do not quickly coalesce.

- Subgroup: Any subdivision of a school. Subgroups apparently form for a variety of reasons. We have recognized ones related to age, sex, nurture, feeding and defense.
- Bout: Any episode in which a dolphin engages for a significant period of time in a single behavior pattern, alone, or with another animal or animals. Usually such bouts are marked by recognizable onset and termination behavior.
- School Envelope: The outside three dimensional shape of a school.
- Newborn: Up to about 105 cm total length; fetal folds (may or may not be evident; they are faint at best in spinner dolphins), folded fins or flukes.
- Calves(less than 1 year old): Less than $3/4$ of adult total length (105-128 cm, approx.) Typified by a head relatively larger than adults, smaller fins, juvenile locomotion and less boldly marked color pattern than in adults.
- Subadult: Length approximately 128-170 cm. Approaching adult proportions and locomotion patterns. Fins still noticeably small and bodies less robust than adults.
- Adult: Length greater than 170 cm (Perrin 1975b). Relatively small head, tall dorsal fin, postanal protuberance and thickened tail stock present in males.

RESULTS

Distribution

Spinner dolphins occur throughout the Hawaiian Island chain, from Kure Atoll southeast to Ka Lae, the southernmost point of the Island of Hawaii (Norris and Dohl 1980). Distribution around the various islands is not random. Schools tend to congregate habitually in certain areas and there appear to be seasonal changes in abundance from area to area.

Our aerial survey data taken along the shore of the Island of Hawaii were analyzed by dividing the island coast into three main sections and nine subsections. These sections represented coastlines within which seasonal weather regimes were relatively uniform, allowing us to check for seasonal population shifts. The regions distinguished in this way are:

- (1) North Hawaii, made up of (a) Kiholo Bay to Upolu Point, and (b) Upolu Point to Hilo;

(2) Southeast Hawaii, made up of (a) Hilo to Cape Kumukahi, and (b) Cape Kumukahi to South Point, and;

(3) Kona, consisting of (a) South Point to Lepeamoa Rock, (b) Kauhako Bay to Palemano Point (c) Kealake'akua Bay, (d) Keaweakeheka Point to Kaiwi Point, and (e) Honokohau to Kiholo Bay.

The non-random nature of spinner dolphin distribution is clearly shown by examining data from these various subsections of our aerial survey. The Kona coast accounts for 75% of the 98 sightings. Southeast Hawaii accounts for 16% and North Hawaii for 9%. The survey makes it clear that within the three main sectors of the aerial survey, certain bays or shoal areas are repeatedly occupied while others are only infrequently visited, or not occupied at all. Seasonal patterns also exist (Figures 12, 13).

The distribution patterns for the entire island are shown in Figures 7-11. Sightings in the North Hawaii and Southeast Hawaii sections are concentrated during January and February at the same time the number of sighted animals decreased along the Kona coast. We concluded that the distributional patterns of spinner dolphins around Hawaii could possibly be related to a number of factors, including physiography, distribution of prey, prevalent sea state (do they avoid rough water?), water depth nearshore, type of bottom, and possibly the presence of significant levels of marine pollution. We now describe each coastal section with these factors in mind.

1. North Hawaii

In the region between Kiholo Bay and Upolu Point spinner dolphins were sighted only six times, with no more than one sighting per flight. During the winter months each such sighting consisted of 90 or more dolphins; during the summer there were about 50 or fewer dolphins per sighting. All of these sightings were north of Kawaihae, along relatively exposed coast devoid of shallow bays typical of rest sites elsewhere. From radio tracking we know that the island slope between 100-1000 fathoms is an important feeding ground along some parts of the coast, especially where the escarpment is relatively steep. Here, while the 100 fathom contour is near shore, the 1000 fathom contour is the farthest from shore of any stretch of the island shore (as distant as 40 km). During aerial surveys around the island dolphins were sighted on the average 10.0 km ($\pm$ s.d 6.83 km, n=90 sightings) from the 1000 fathom contour. It may be that this sector of the escarpment is insufficiently steep to provide characteristics responsible for spinner use elsewhere, or perhaps the deeper waters are too far offshore to make regular transits energetically feasible.

The region between Kiholo Bay and Kawaihae, where we saw no dolphins, includes some of the most protected bays along the

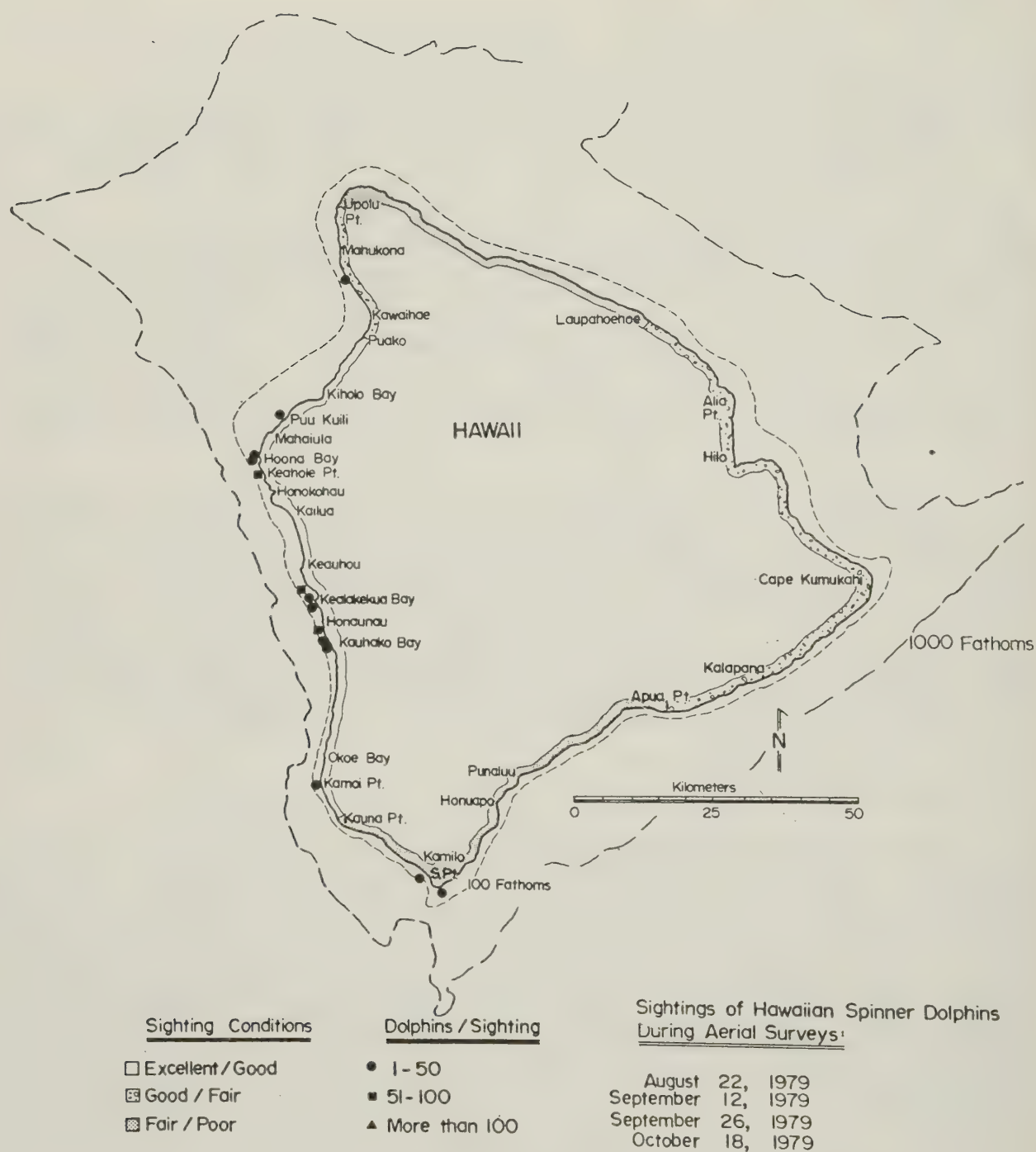


Figure 7. Distribution of spinner dolphin sightings during aerial surveys, August 22-October 18, 1979. Typical sighting conditions are indicated along shoreline, and 100 and 1000 fathom contours are shown.

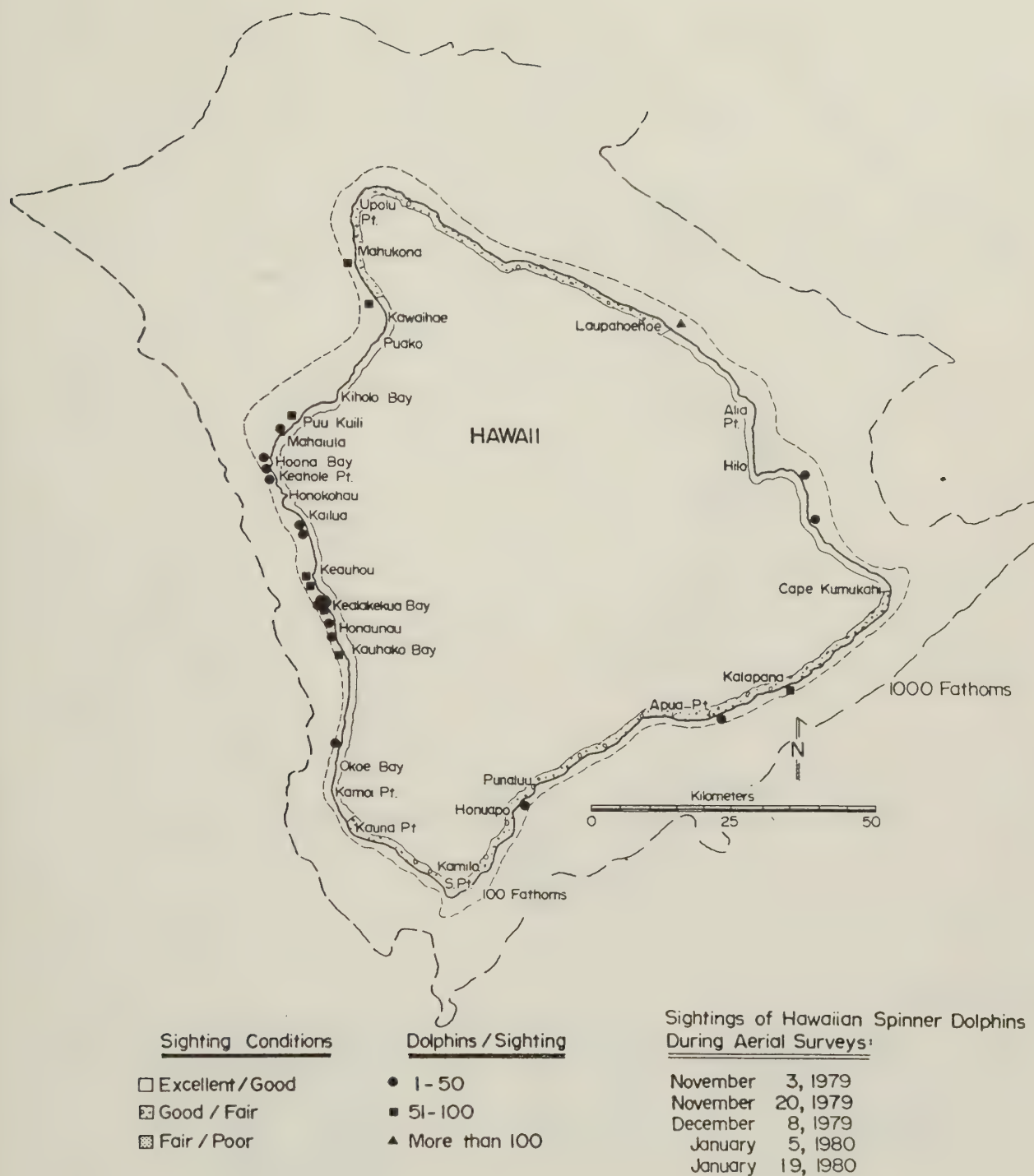


Figure 3. Distribution of spinner dolphin sightings during aerial surveys, November 3, 1979 - January 19, 1980. Typical sighting conditions are indicated along shoreline, and 100 and 1000 fathom contours are shown.

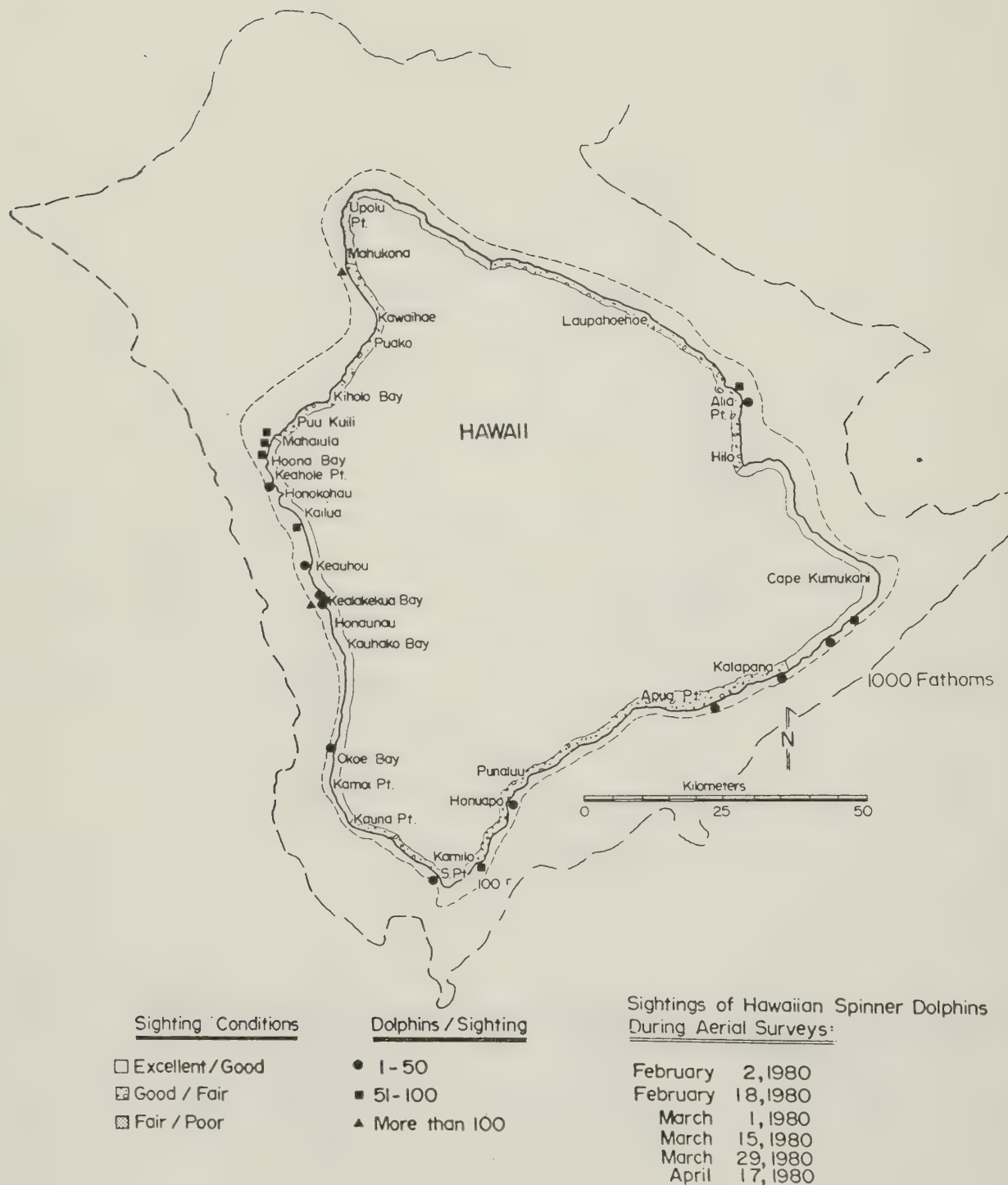


Figure 9. Distribution of spinner dolphin sightings during aerial surveys, February 2 - April 17, 1980. Typical sighting conditions are indicated along shoreline. The 100 and 1000 fathom contours are shown.

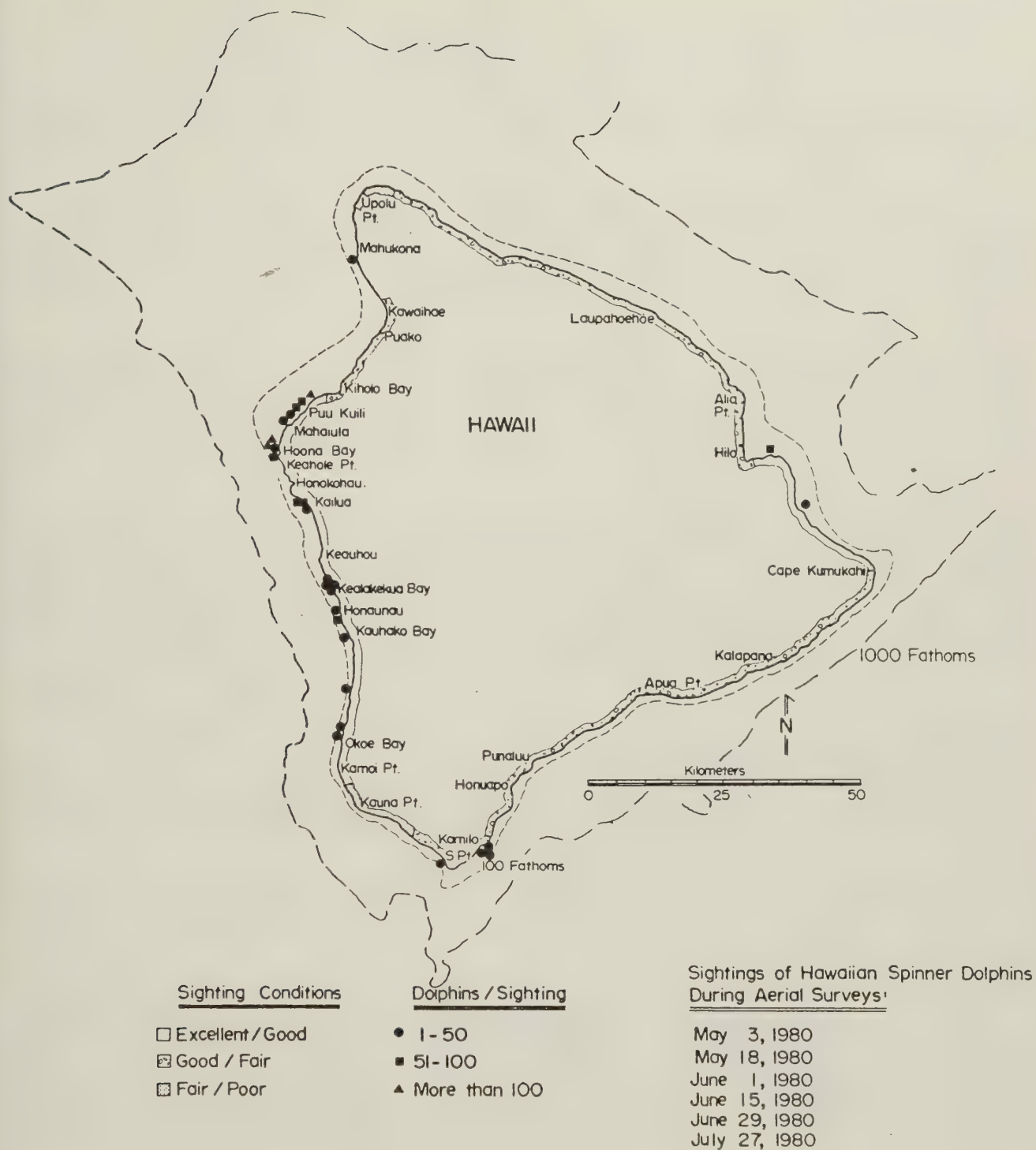


Figure 10. Distribution of spinner dolphin sightings during aerial surveys, May 3 - July 27, 1980. Typical sighting conditions are indicated along shorelines. The 100 and 1000 fathom contours are shown.

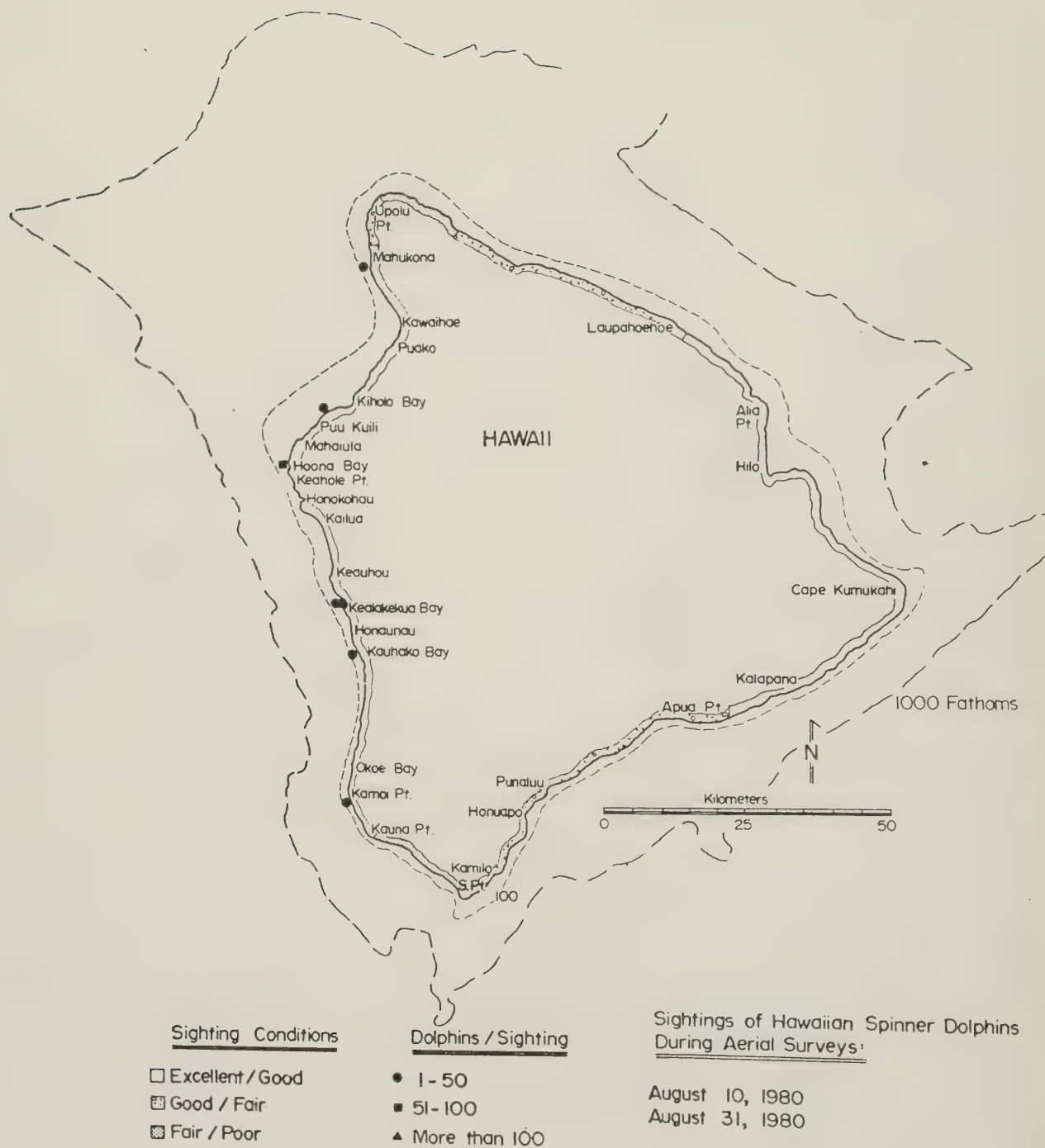


Figure 11. Distribution of spinner dolphin sightings during aerial surveys, August 10 - 31, 1980. Typical sighting conditions are indicated along shorelines. The 100 and 1000 fathom contours are shown.

Hawaiian shoreline but is very distant from deep water feeding areas. Norris and Dohl (1980) also did not sight any dolphins in this area.

The bays of this Kiholo Bay-Kawaihae sector are relatively shallow as compared to those used by dolphins elsewhere, and contain extensive developments of coral heads. More open, sandy flats typify resting places used by spinners elsewhere on the island.

Three spinner dolphin sightings were made between Upolu Point and the town of Hilo; all three occurred during January and February. School size range from 12 to 150 dolphins (mean=93 $\pm$ s.d. 72.2). The sightings occurred when sighting conditions were best. Sighting conditions in this area are generally fair to poor.

Two of three sightings were of large groups and occurred at the same time as large groups were sighted elsewhere outside the Kona sector. Kona, for comparison, produced fewer animals than at any other time of year, suggesting that a seasonal movement of animals had occurred away from Kona. This "movement" occurred at the time when calves made up the smallest proportion of dolphin schools sighted, and was outside the apparent breeding season (Figures 12, 13).

A possible explanation is that schools of spinner dolphins with calves tend to remain in regions of relatively calm water. The number of dolphins seen off the Kona coast increases after winter, suggesting, but by no means proving, that dolphins return to calmer water at the onset of breeding season.

This circumisland movement is supported by the sighting of a marked animal seen on the Kona coast and then at Hilo on the opposite side of the island (see Distribution, 3. Kona).

The island sector from Upolu Point to Hilo has other apparent detrimentals that could affect dolphin presence. It is an area of rough seas. It is typified by a rather broad, gradual slope out to the 1000 fathom contour, and the waters are often heavily polluted. Runoff from sugar cane processing plants often discolors water up to a kilometer offshore, and rafts of sugar cane waste (bagasse) are common. Norris and Dohl (1980) did not report any sightings from this section of coast.

2. Southeast Hawaii

Aerial surveys provided only four sightings of spinner dolphin schools between Hilo and Cape Kumukahi. The schools ranged in size from 21 to 55 individuals (mean=34 $\pm$ s.d. 15.2), and were observed once each during November, December, June and July. An

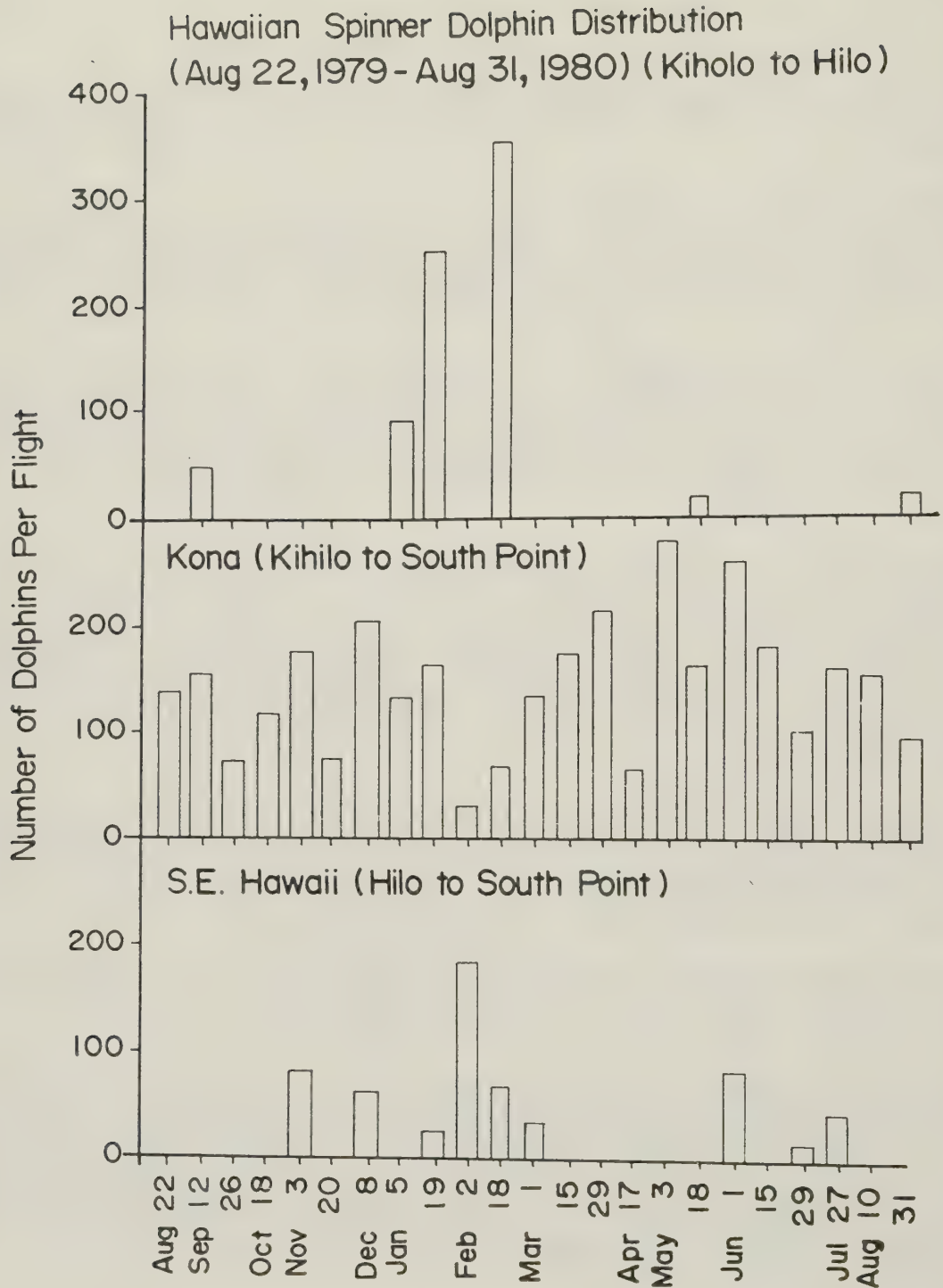


Figure 12. Seasonal distribution of spinner dolphins seen during aerial surveys, by coastal section. The numbers are minimum observer estimates, or counts from photographs. The three sections are described in the text.

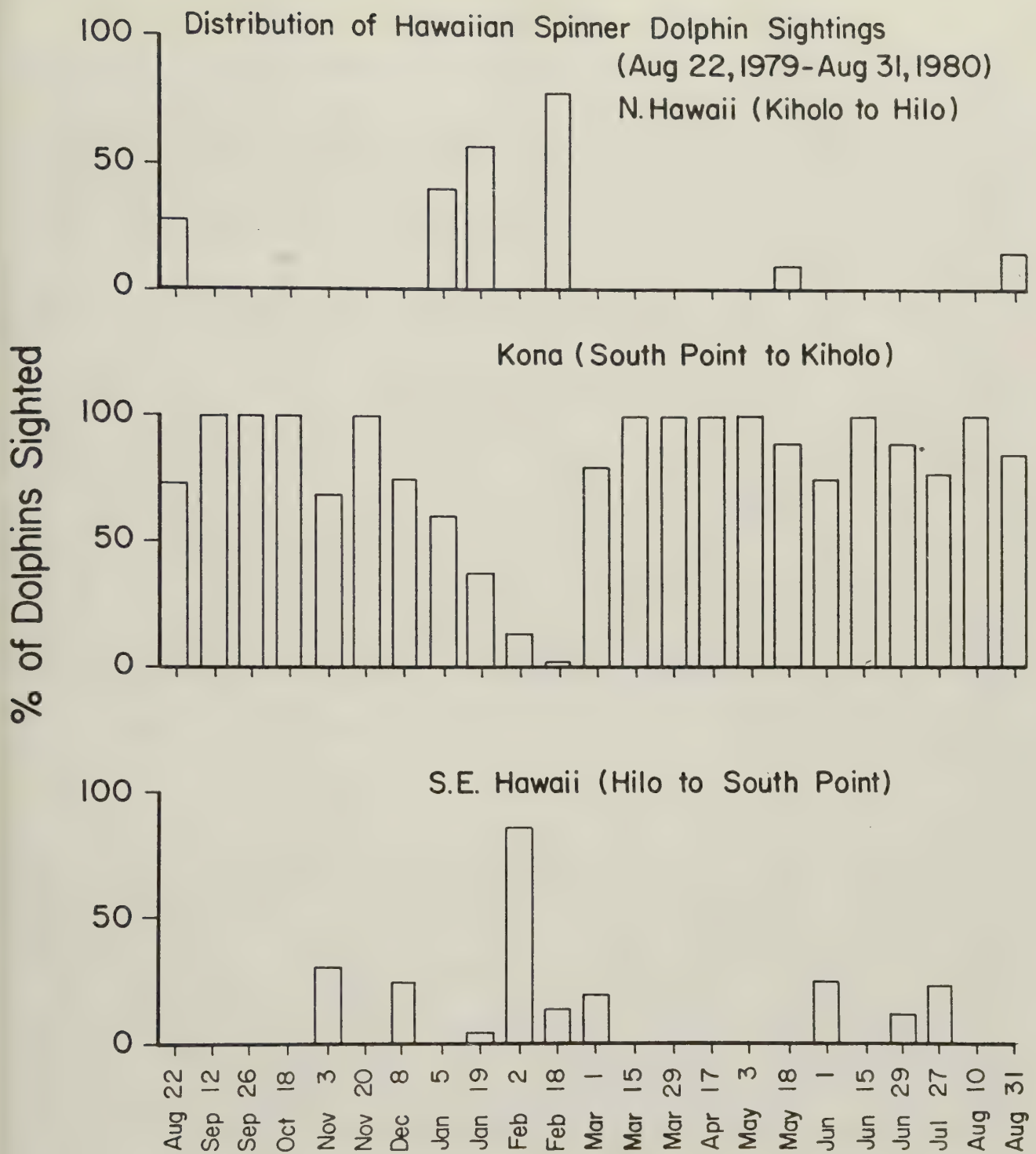


Figure 13. Seasonal distribution of spinner dolphin sightings during aerial surveys as a percentage of total sightings. The numbers of dolphins seen are minimum observer estimates, or counts from photographs. The three sections are described in the text.

additional June 1981 record was made on a photographic identification expedition to Hilo.

The animals were generally located in small bays near Kaloli Point or Leleiwi Point. Even within these bays the water tended to be rather rough, as the shore is exposed to the northeast trade winds. These bays are within 5 km of the 1000 fathom contour. Norris and Dohl (1980) found a school of about 100 dolphins in a bay near Kaloli Point.

Twelve spinner dolphin sightings were recorded from the 100 km coast between Cape Kumukahi (the southeast corner of the island) and South Point (the southwest corner). Sightings occurred at all seasons except August-October. The animals occurred in groups of 11-80 (mean=38 $\pm$ s.d. 19.9), and were generally in larger groups in the winter than at other seasons. The dolphins were most often found in the small bays to the southwest of Punaluu or to the northeast of Apua point. In this region the 100 fathom contour is near shore but the 1000 fathom contour is the farthest from shore along this coast (up to 26 km off Keaoi Island). This entire region is generally exposed to rough seas associated with high winds. Conditions are generally worst during the period August-October. Norris and Dohl (1980) reported several small schools in rough water between South Point and Honuapo, near Kaalualu, in the protected waters off Keaoi Island, and off Opihikao (reported by them as "Opilukao"). Their sightings were generally consistent with those of the present study except that we never saw dolphins near Keaoi Island during our 23 surveys.

3. Kona

The south Kona region extends from Lepeamoa Rock, just south of Kauhako, southward to and including the water off Ka Lae, or South Point. Dolphins were sighted 11 times in this region, during all periods but December-mid March. Group size ranged from 4-40 dolphins (mean=21 $\pm$ s.d. 11.9). Dolphins were generally found in smaller groups in this region than in any other area. They were most often found resting in the shallow protected bays near Miloii (Okoe Bay), near Kamoi Point, off South Point, or traveling between Lepeamoa Rock and Okoe Bay very close to the shoreline. The 1000 fathom contour is typically within 5-10 km of shore in this region. From Kauna Point southward to within several km of South Point the 1000 fathom contour is as much as 15 km from shore. No dolphins were sighted in this small area, but sighting conditions were consistently worse there than in other parts of the south Kona region. Norris and Dohl (1980) believed that the south Kona region did not harbor dolphins on a regular basis, but they were unable to fly over this region regularly.

Eleven sightings of spinner dolphin schools were made between Lepeamoa Rock and Palemano Point. Sightings occurred during all months except March-May. Sighting conditions were excellent in this area throughout the flights. The animals were usually found in one of two shallow bays; Kauhako Bay or Alahaka Bay. No seasonal trends in group size were noted; school size range from 6 - 98 dolphins (mean = $38 \pm \text{s.d. } 25.0$). The 1000 fathom contour is within 8.5 km of shore in this region. During radio-tracking, dolphins generally remained close to shore in this area in less than 800 fathoms of water.

Kealake'akua Bay provided 15 sightings, during all seasons. School size ranged from 4-91 dolphins (mean = $33 \pm \text{s.d. } 27.0$), with the fewest present when numbers were highest on the east coast (see Figure 12). School sizes observed during aerial surveys are comparable to those recorded from the bay by other means. Kealake'akua Bay is the most protected large bay on the island, providing shallow waters in which the dolphins are frequently found resting. The bay is less than 11 km from the 1000 fathom contour. Norris and Dohl (1980) found spinner dolphins in this bay on 74% of their observation days, in schools ranging from 7-70 dolphins. In our observations dolphins entered the bay on 258 of 328 scan days, or 79% of the time. We deal with data from this bay extensively elsewhere in this report and will not discuss it further here.

Spinner dolphins were sighted on 11 occasions between Keaweakehaka Point, at the north limb of Kealake'akua Bay, and Kaiwi Point, near the small boat harbor of Honokohau. These sightings occurred during all months but August-November (though we have numerous sightings from boat surveys and radiotracking during these months). Dolphin school size ranged from 13-81 animals, without any obvious seasonal trends. Typically the dolphins were travelling slowly along this coast, although they were occasionally seen milling in Maihi Bay, or just off the town of Kailua. Maihi Bay is a very shallow relatively unprotected indentation of the coast. Nearby Kailua Bay offers a deeper, more protected indentation, with a shallow, sandy bottom much like Okoe Bay, or Kamoi Bay to the south. The inner reaches of Kailua Bay, which are typically filled with sport and tourist boats were not used by dolphins. Waters in the general vicinity of Kailua Bay are quite murky compared to other sections of the Kona coastline. The only other significant bay along this stretch of coast is at Keauhou. This small narrow bay is well protected and shallow but is utilized as a mooring area, and no dolphins were seen inside this bay.

The waters in this area are generally quite calm, and the 1000 fathom contour is within 5-10 km offshore.

The north Kona region from Honokohau Harbor to Kiholo Bay most consistently provided sightings of spinner dolphins. Dolphins were present in this region during all months but February

(at which time they were present along the North Hawaii and Southeast Hawaii coasts). Schools ranged in size from 14 to 180 dolphins (mean = $63 \pm$ s.d. 44.2), and were larger during March-June than at other times.

The dolphins were most frequently seen milling in Hoona Bay, the small bay just north of Keahole Point. This bay does not afford much protection, but allows quick access to the steep underwater escarpment off Keahole Point. The 1000 fathom contour is only 6.5 km offshore, but to the northwest this contour trends rapidly offshore until at Mano Point, it is already 23 km offshore.

Radiotagged dolphins were followed offshore over "the grounds", as the local fishermen call the region off Keahole Point between the 100 and 1000 fathom contours, both during this study and the earlier work of Norris and Dohl (1980)

Typically, dolphins were seen in the shallow bays to the north of Keahole Point during the morning, slowly traveling southward, with occasional periods of milling. In the afternoon schools frequently moved into Hoona Bay (usually from the north but sometimes from the south) prior to heading offshore in the evening.

Norris and Dohl (1980) estimated that there were 200-250 dolphins generally occurring in this area, either in a single school or fragmented into smaller schools separated by a few kilometers. These observations were consistent with ours. The animals comprising this 200-250 dolphin "population" are not however restricted to the north Kona area. Radiotracking and observation of naturally marked animals show that the same individuals seen at the Keahole Point area may be found from near Milolii, near South Point and as far north as Mahukona near the north point of the island, and even entirely around the island near Hilo.

Clearly, particular regions or bays have upper limits to the number of animals they seem able to accomodate. The 200-250 dolphins sometimes found near Keahole Point seems to represent a "carrying capacity" of the region at any one time, though many or most of the 900-1000 dolphins estimated to occur on the entire Island of Hawaii coast may pass through the area from time to time (see Abundance).

4. Interpretations

Physiography appears to play the dominant role in the distribution of spinner dolphins around the coast of the Big Island. Fifty-three percent of the dolphin sightings were within bays. Such bays ranged from several hundred meters broad to 4 km across. The animals clearly aggregate in them preferentially.

The bays amount to much less than 53% of the coastline, and many bays that seem prime habitat from the surface seldom or never hold animals.

The slope of the sea floor and the nearby presence of steep escarpments, providing quick access of offshore feeding grounds, seems a primary determinant of bay occupancy. The greatest concentrations of dolphin sightings were in areas with relatively easy access to these drop-offs, while few or no dolphins were sighted in those areas where the drop off was more gradual or distant from the shore.

Sea state may influence distribution but this is difficult to document because sea state also influences our sighting ability. But some support for this idea derives from sightings of schools in some areas that are normally subject to poor conditions during calm weather months, and at the same time schools were absent from areas where they were usually found. Also, large schools are often visible under less than ideal conditions. We would not expect to miss them in our surveys.

The vast majority of dolphin sightings were typically in calm, protected lee waters. The extensive use of shallow, sandy bottomed bays or shoal areas nearshore seems borne out as well. These facts, taken together with close access to feeding areas, make most sightings understandable.

Activity Patterns

The daily sequence of activity patterns of the Hawaiian spinner dolphin has been described by Norris and Dohl (1980). Here, we add much detail to these observations and provide some modifications and extensions of the earlier perceptions.

Dolphins entered Kealahou Bay in alert rapidly moving schools in the morning and then descended into a rest period during which they swam slowly, deep in the bay. In the afternoon they aroused and began sorties of fluctuating speed and activity level that we call zigzag swimming. Toward late afternoon or dusk the pattern changed as the school rapidly moved out the bay, only to disperse once deep water was reached. Then the school entered a presumed feeding pattern, moving slowly along and diving over the island slope 100-1000 fathoms below (Table 2).

Figure 14 shows the average time of day at which dolphin schools entered the bay during different months. There is a significant linear relationship between sunrise and the time of entrance ($r^2 = 0.32$, slope = 1.14, intercept = 0.4, $n = 13$) with the average entrance time 1 hr 12 min (s.d. $\pm$ 1.66 hr, $n = 109$) after sunrise. During the fall and winter months (October-March) dolphins entered the bay significantly later than during the rest of the year (Analysis of variance, Student Newman-Keuls Multiple Comparison Test, $p < 0.001$).

Table 2. Average speed, water depth, and time of day dolphin schools entered inner Kealake'akua Bay, moved within the bay and exited.

Speed (km/hr)			Depth (m)	Time of Day
Enter Bay	$\bar{x}$	4.9	30.9	0730
	s.d.	3.0	27.09	1 hr 44 min
	n	10	10	106
Inside Bay	$\bar{x}$	2.6	21.3	--
	s.d.	2.68	8.95	--
	n	3811	4151	--
Exit Bay	$\bar{x}$	5.9	39.4	1442
	s.d.	4.00	33.36	2 hr 58 min
	n	18	18	85

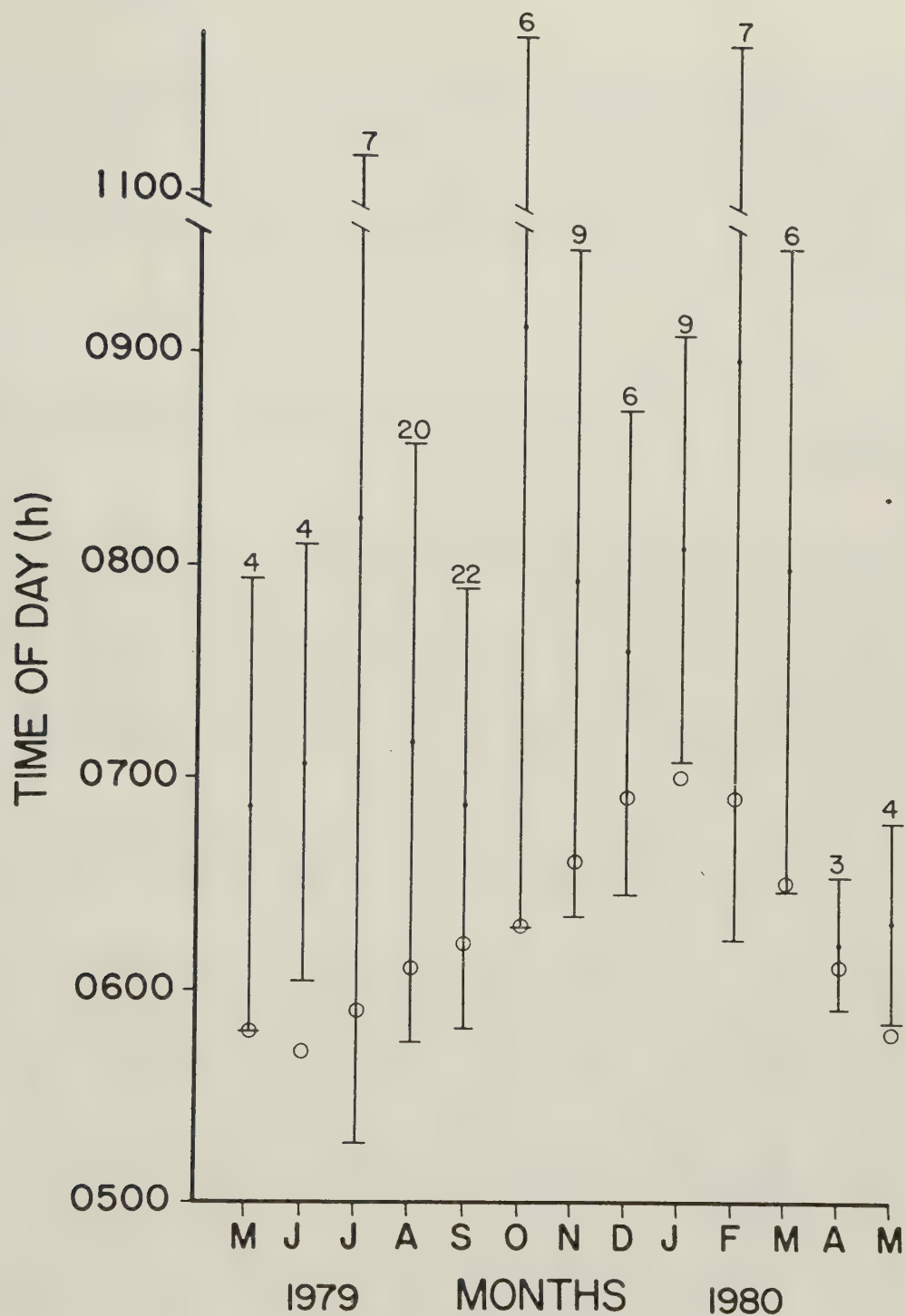


Figure 14. The average time of day of dolphin entry into Kealake'akua Bay, by month. Bars show means and standard deviations, numbers above them are sample sizes. The small circles show average time of sunrise.

There proved to be a dramatic seasonal change in the amount of time spent per day in Kealake'akua Bay. Only about 4-5 hours per day were spent in the bay in winter, and 7-9 hours per day during spring (Figure 16). Figures 14 and 15 show details of these differences. In spring dolphins tended to enter early and leave late. In summer they entered not quite as early and they left quite early. May was the month of longest average daily residence in the Bay.

1. Interpretations

The seasonal residence time in Kealake'akua Bay invites explanation. But at this time only a series of possibilities can be suggested.

The pattern is clearly seasonal and generally tracks the annual cycle of daylength, though longest residence was found to be in May, or before the longest days. Arrival and departure relations are less clear. Earliest arrivals in our data generally match the shift from nighttime darkness to daylight, but the reader is cautioned to remember that before dawn our observers could not see (Figures 14, 15). The pattern of shoreward movement probably begins in the early morning hours of darkness as animals tend to move shoreward from nighttime feeding grounds (Norris and Dohl 1980).

The extreme times of departure tend to be well before sunset in winter. We feel confident of this relationship since our observers tracked schools prior to the end of day and were able to follow them as dusk fell.

Mean arrival and departure times are very variable, and no clear trends emerge. This is probably due to heterogeneous variation in our data. Two or more activities are probably masked in a single measure. For example, since spinner dolphins feed on scattering layer organisms that rise from deep water near dusk, food sources are not available while the sun is high. Hence movement to the feeding grounds seems not to take place until near dusk. But other movements and activities may occur between the time of arousal and departure. In long days the rest period may not need to consume the entire day and dolphins have been noted moving out of the bay before dusk, and instead of going directly offshore, moving along the coast before angling out into deep water. The precise measure we need is when schools moved from near land to feeding grounds and our data do not provide it.

Another probable source of complication is that while the rest period may possibly be of rather uniform length throughout the seasons we could not always determine its length with precision. Various subgroups in schools frequently seemed to be in different stages of alertness. During short winter days it is possible that dolphins consumed most or all of their residence

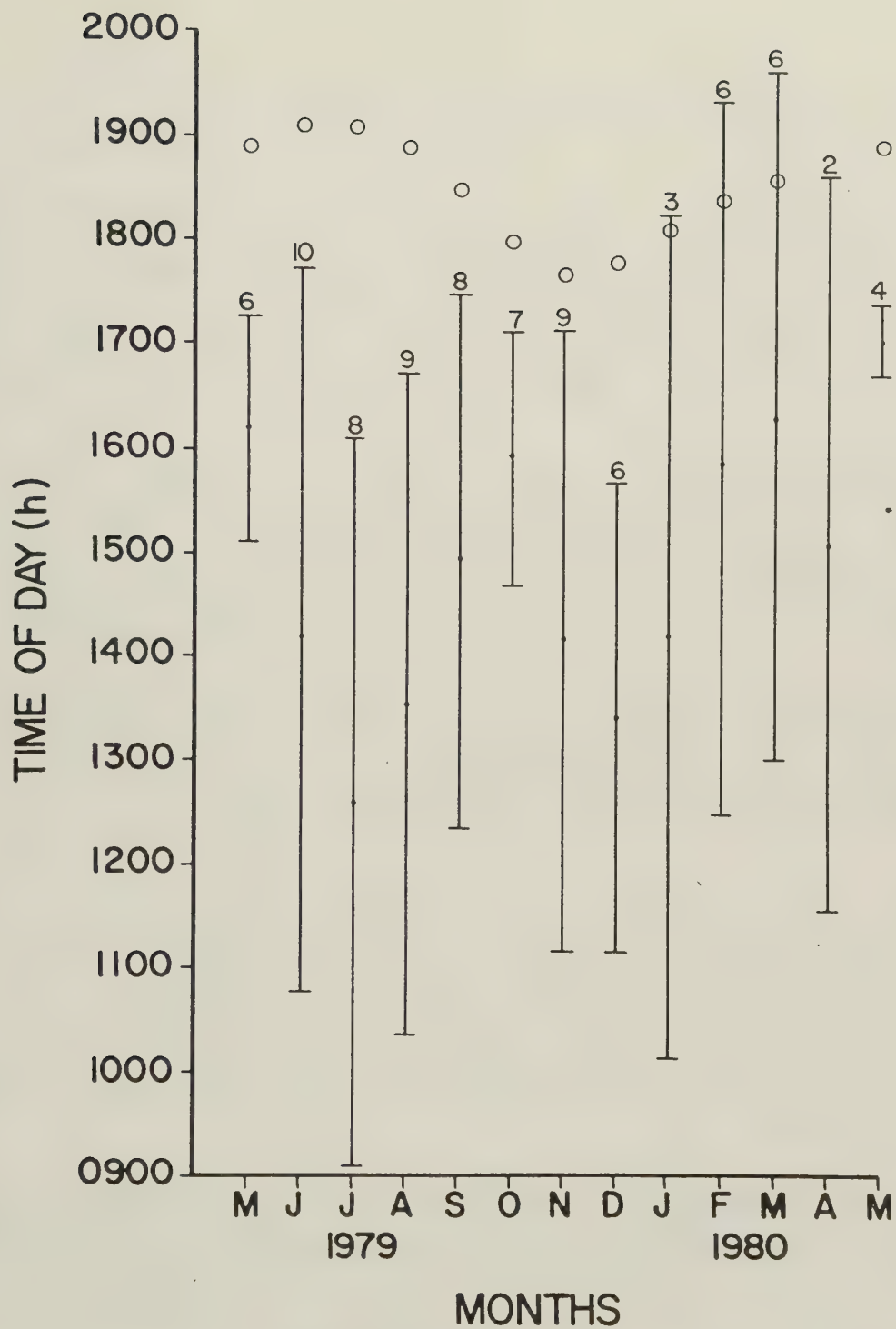


Figure 15. The average time of day of dolphin exit from Kealake'akua Bay, by month. Bars show means and standard deviations, numbers above them are sample sizes. The small circles show average time of sunset.

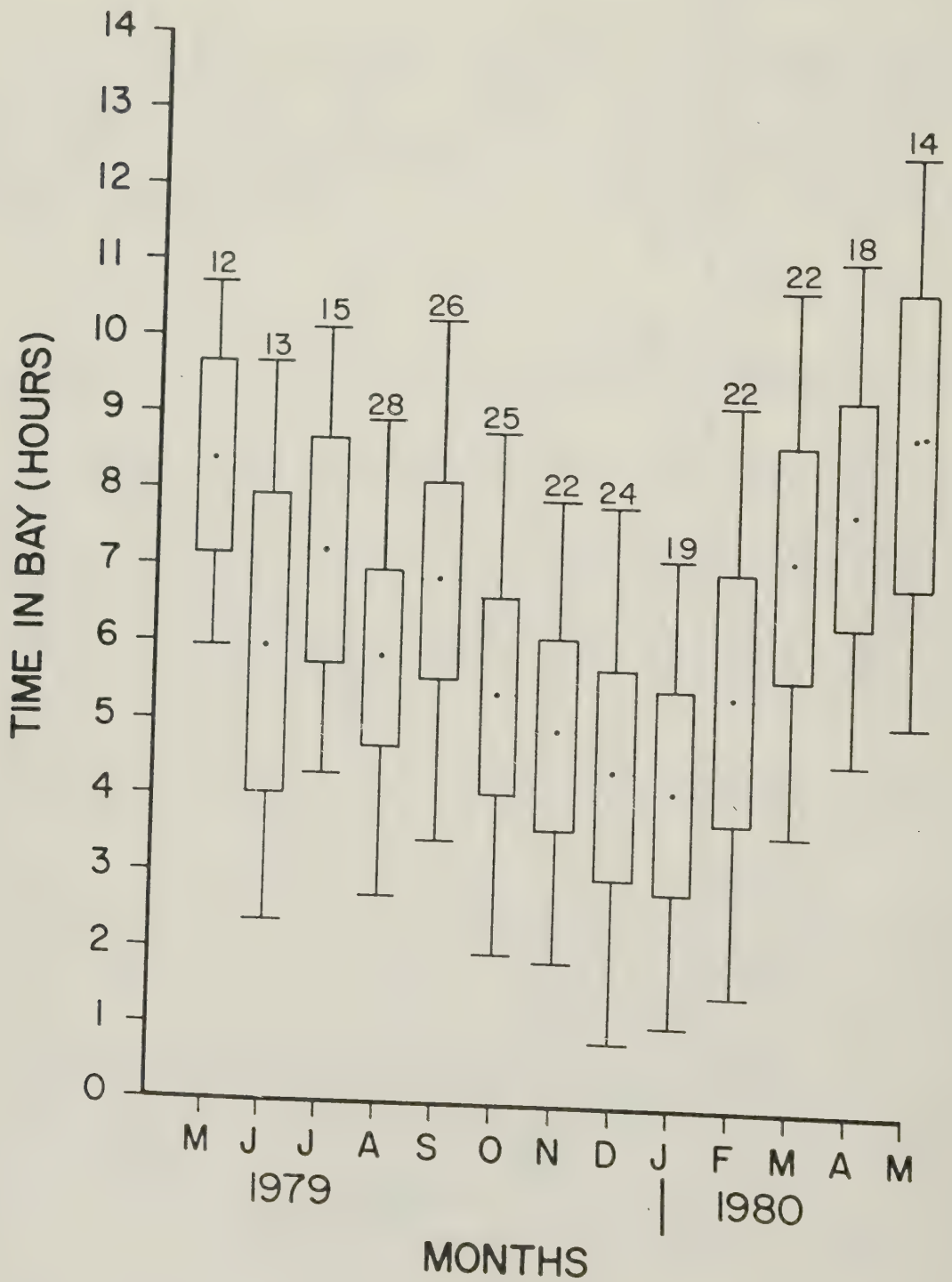


Figure 16. The average amount of time dolphins spent per day in Kealake'akua Bay, by month. Bars are as in Figure 13. The boxes represent 95% confidence intervals.

time in rest while in longer spring and summer days part of the longer residence may have been by animals that were fully aroused and active and alert within the bay.

A final complication seems to be that not all schools entering the bay do so from directly offshore. Some seem to make landfalls elsewhere along the coast and to travel some unknown distance alongshore before arrival at Kealake'akua Bay. Events offshore could relate to this and secondarily to residence time. If food is more available at one season than another in a given area, less time may be required for hunting and more therefore made available for stays alongshore.

The peak length of time in the bay corresponds with peak recruitment offshore of larval reef fishes (and fishes and squid feeding on them) during April and May (Phillip Lobel, Harvard University, personal communication). This may mean that dolphins need to spend less time outside the bay feeding than at other times. Unfortunately we know very little about what the seasonal diet of spinner dolphins is (see Food).

The average number of dolphins per school to enter Kealake'akua Bay was 33 (s.d. ± 19.6 , $n = 234$). School size fluctuated on a seasonal basis, with generally fewer animals present during winter than any other seasons (Figure 17). There is a linear relationship between time spent in the bay by season and school size per month, by season. ($r^2 = 0.378$, slope 0.180, intercept = 0.361, $n = 121$).

The average school size of 30 animals squares with a subjective impression that schools of about that size were the most cohesive and settled into rest more resolutely than either small or larger schools (Figure 18). The larger schools tended to split into two smaller schools, while small schools seemed more wary and easily disturbed. Very small schools were apt to be elusive and to resist attempts to observe them closely (Norris and Dohl 1980). We will return to this question later in the paper.

Before we examine the daily activity pattern in detail, a few more general seasonal and diurnal characteristics will be described. Overall, dolphins traveled at roughly the same speed (mean speed 2.6 km/hr, s.d. ± 2.7 , $n = 3811$) as they moved back and forth during the rest period. But, in the afternoon, as they began zigzag swimming, average travel speed almost doubled to 4.7 km/hr (s.d. ± 4.6 , $n = 24$) (Figure 19). These measures of extreme difference mask more subtle changes in school behavior. For example, the 10:00-11:00 time period includes groups that have just arrived in the bay and were still active, those that were already quiescent, and even some that were about to leave.

There was no consistent seasonal difference in speed of travel while in the bay although average speeds by month were not

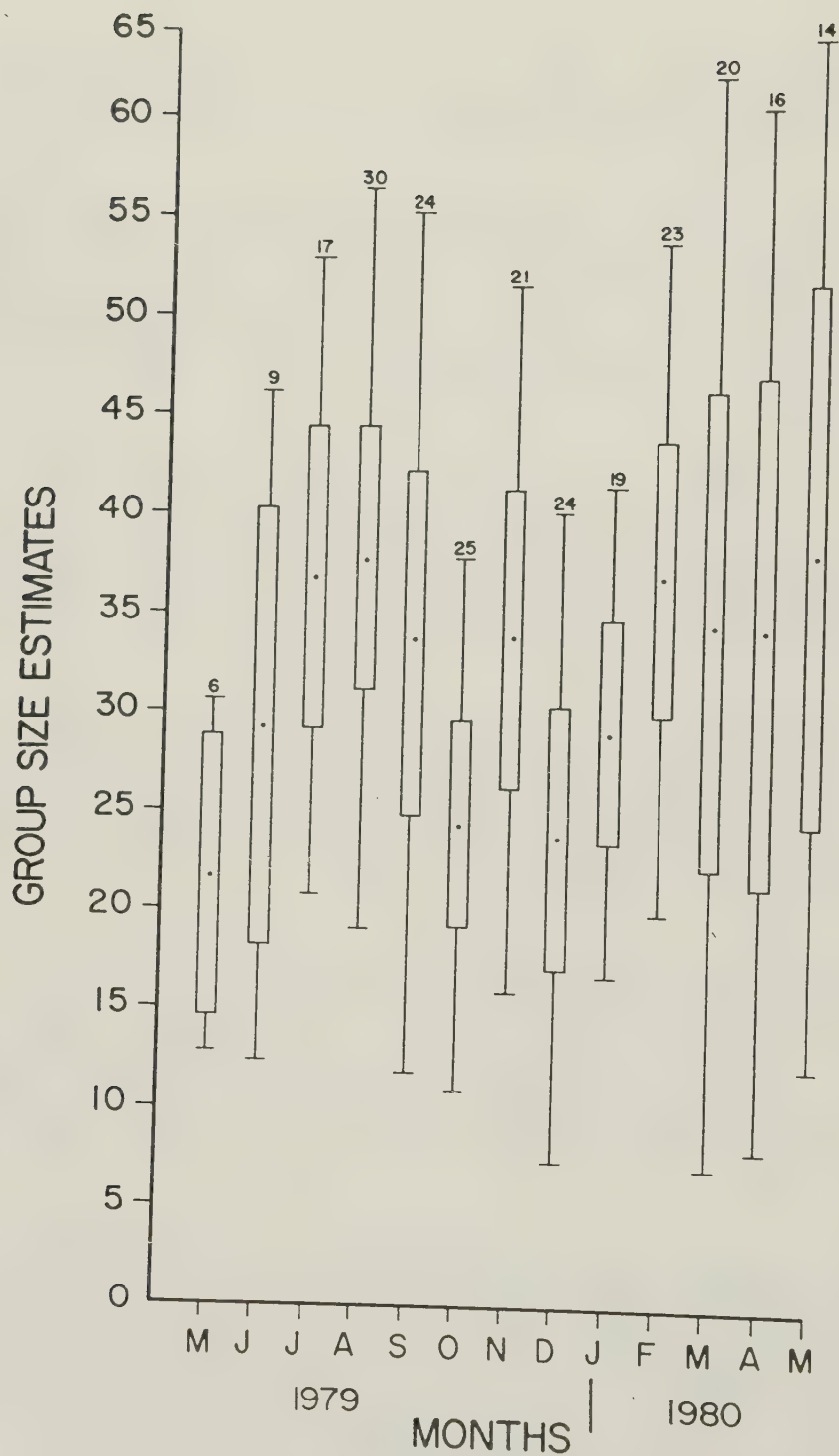


Figure 17. The average group size of spinner dolphins to enter Kealake'akua Bay, by month. Bars are standard deviations. The boxes represent 95% confidence intervals.

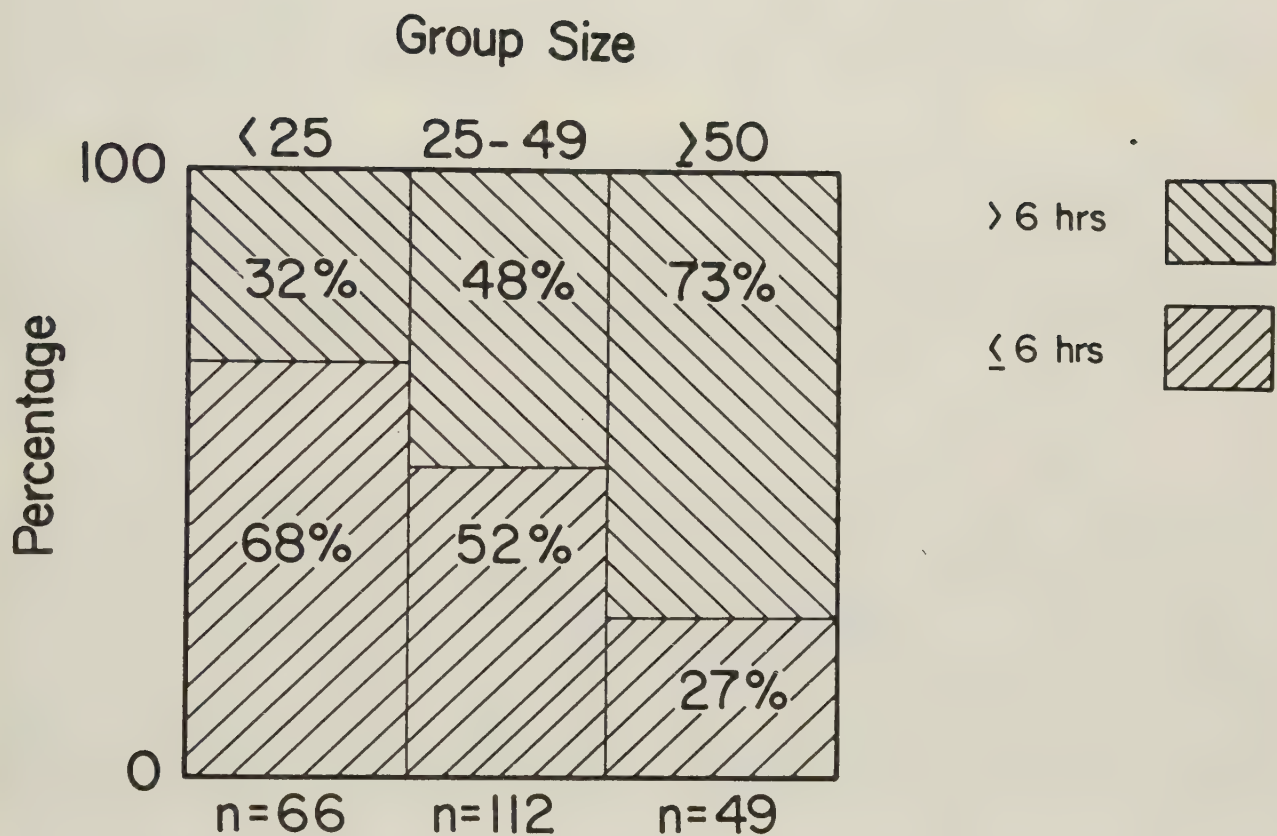


Figure 18. The relation of school size and residence time in Kealake'akua Bay. Those schools staying six hours or less are contrasted with those staying more than six hours; for three sizes of schools.

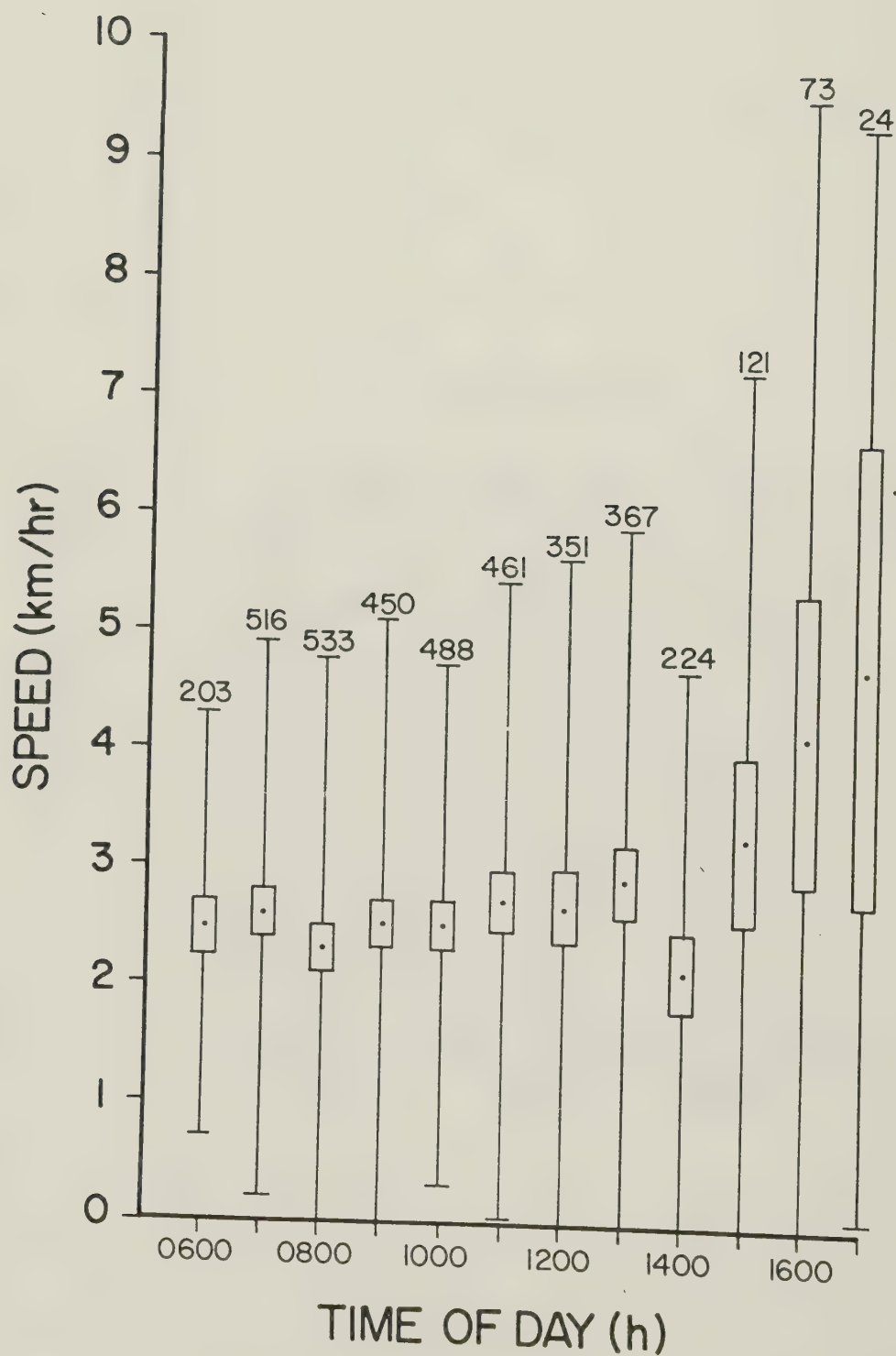


Figure 19. Average speed of travel of dolphin schools, by time of day. From theodolite data. Bars are standard deviations. Boxes represent 95% confidence intervals.

uniform throughout the year (Analysis of variance, $n = 3811$, $p < 0.001$)

There was no consistent seasonal difference in the depth of water over which dolphins traveled while in the bay (Figure 20). Zigzag swimming certainly contributed to the scatter in this measure since it takes dolphin schools back and forth between shallow and deep water in seemingly erratic fashion. Since there was an increase in speed late in the day (Figure 19) it is not surprising that there is a significant linear correlation between speed and depth ($r^2 = 0.667$, $p < 0.05$). In summary, dolphins moved more rapidly late in the afternoon and did so more often in deep water.

A sample plot of the usual movements of a school of dolphins is shown in Figure 21 and Table 4, and a plot of dolphin location, summarized for the first year of theodolite tracks, is shown in Figure 22. Table 2 presents summary data on dolphin speeds, depth of water while traveling in the bay, and the time of leaving and entering Kealake'akua Bay, as derived from theodolite tracks in the bay.

Aerial Behavior

It has been proposed (Norris and Dohl 1980) that the aerial activity of spinner dolphin schools provides a general means of assessing the activity level of a school. They divided aerial activity into seven different patterns; spins, arcuate leaps, tail-over-head leaps, backslaps, headslaps, noseouts and tailslaps. To this list we add a seventh clear class; the salmon leap. Not only can the general activity of spinner schools be judged by the overall frequency of aerial behavior but the various classes can be arranged in a rough activity order, allowing an even more refined assessment of school state by the surface observer.

Typically, outside Kealake'akua Bay aerial behavior was usually to be seen. Once inside the inner headlands (Manini Point) aerial activity ceased for a time. Most schools entered from the south (71%, $n = 104$) and then moved in a rather straight line toward the rest area. Approximately 1.2 hours after passing the inner headlands and continuing for about two hours aerial activity declined and often was absent for long periods. In the late afternoon the dolphins became active once again, and increased their surface activity until it reached a high about 10 hours after entry (Table 3).

Those groups that stayed in the bay for a briefer period than the average, tended to condense this pattern but continued to show a decrease in aerial activity during the approximate midpoint of their stay.

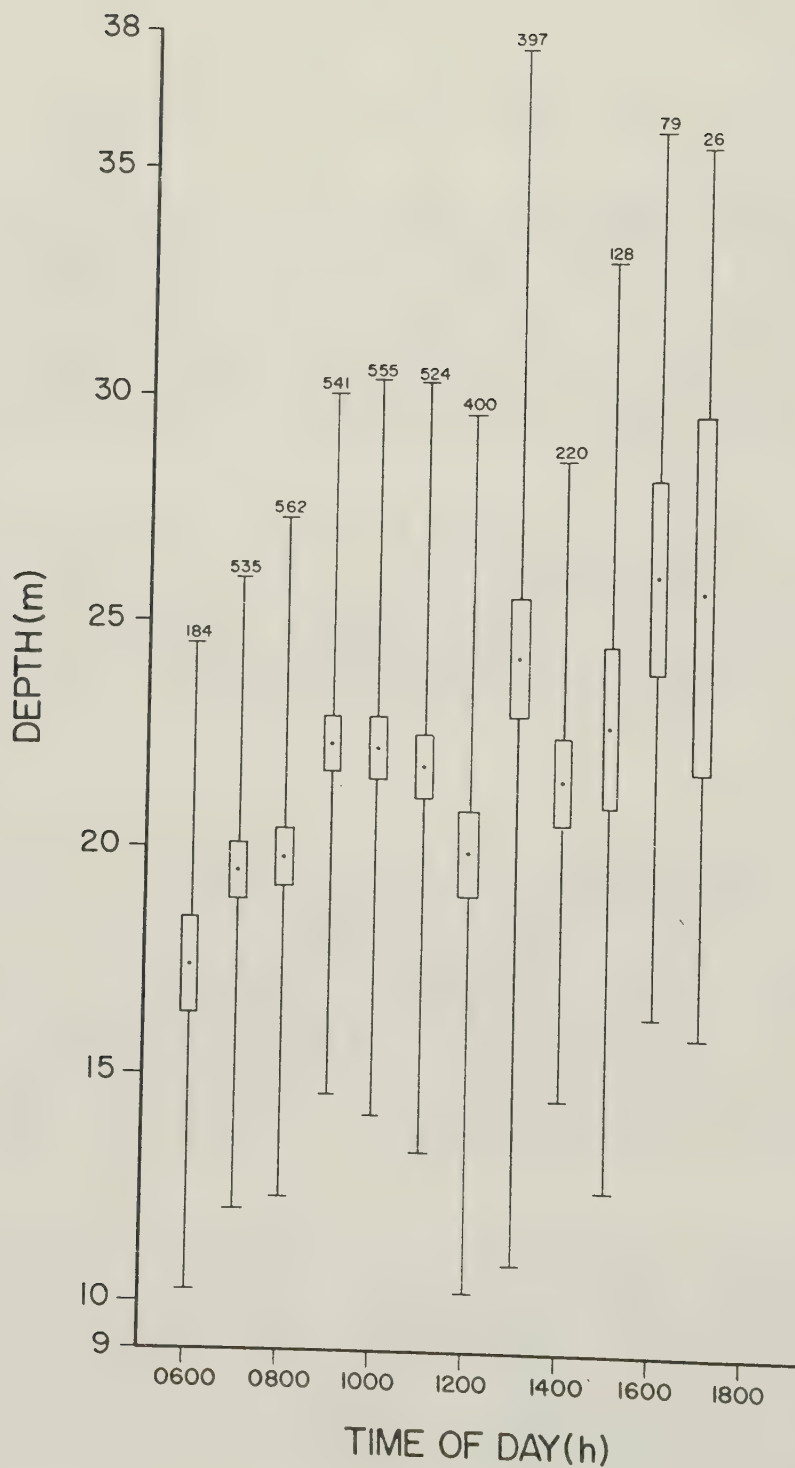


Figure 20. Average water depth over which dolphins traveled in Kealake'akua Bay, as determined by theodolite tracking; by hour of the day. Bars are standard deviations. Boxes represent 95% confidence intervals.

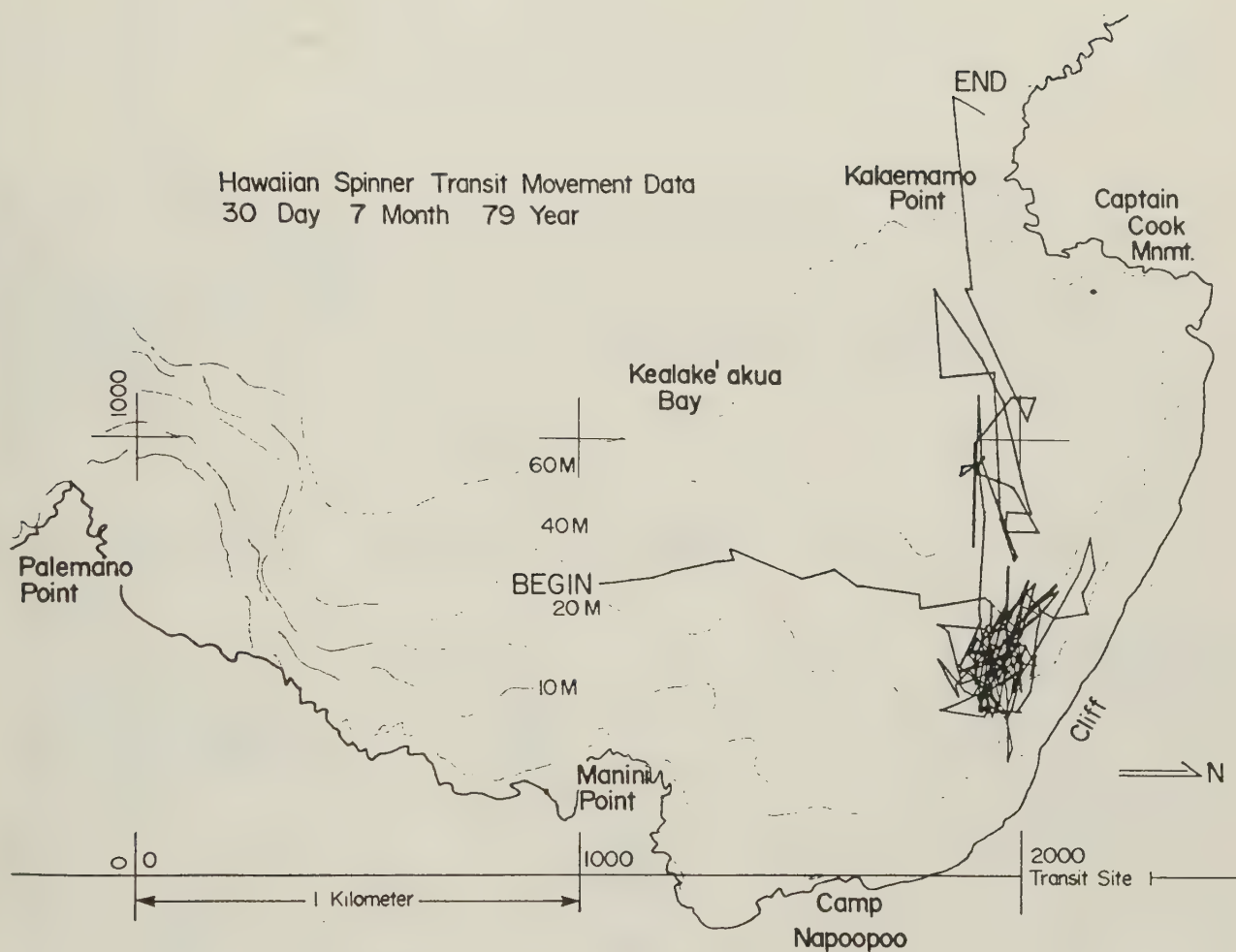


Figure 21. Movement pattern of a 40-60 animal school, July 30, 1979, in Kealake'akua Bay, generated by theodolite tracking. The school was first seen at 0635 and left the bay at 1412. Shown are travel directly to resting grounds, consistent movement over shallow water between 10-20 m depth, followed by zig-zag swimming, and a rapid traverse out of the north limb of the bay. Scale in km is given on abscissa.



Figure 22. The cumulative average position of dolphin schools per hour of the day, for the period from May, 1979 - July 1980; generated by theodolite tracking. Time of day is indicated on track.

Table 3. Frequency of aerial activities seen in Kealake'akua Bay, standardized by animal/hour. Most peaks were diurnally bimodal, with one peak in the morning and one peak in the afternoon. Peaks of activity more than 2X as high as other daily peaks were scored for just that high part of the day, while peaks closer together were scored for both morning and afternoon. Arcuate leaps were infrequently seen and are not included.

<u>Aerial Activity</u>	<u>Frequency/Animal/Hour</u>	<u>Peaks of Activity</u>
Noseouts	0.072	- morning
Tailslaps	0.240	- morning/afternoon
Flips	0.240	- morning/afternoon
Headslaps	0.240	- morning/afternoon
Salmon Leaps	0.360	- afternoon
Side and Backslaps	0.480	- afternoon
Spins	0.600	- several peaks throughout day (see text)

All aerial patterns but the arcuate leap contain a specific movement that generates an underwater and usually an airborne sound. The spin, for example, is concluded by the dorsal fin of the reentering animal slapping against the water. Some aerial patterns at least, are preceded by precursor behavior and followed by underwater patterns upon reentry.

The following are descriptions of each of these patterns.

1. Arcuate Leaps

These clear arcing leaps made by rapidly moving dolphins. As in other species they seem related to improving the efficiency and speed of locomotion (Au and Weihs 1980). That is, the last one or two tail beats, taken while the anterior body is in air and the tail still in water, can take advantage of the lack of significant turbulent drag over the fast moving body in air. At any rate, frightened dolphins may pour from the water in low leaps away from a source of disturbance. These groups seen in air probably represent social subgroups underwater. Such leaps are also common in rapidly moving but undisturbed schools.

2. Noseouts

These are one of the earliest indications of arousal in a resting schools. As arousal begins animals may thrust their snouts out of water. The snout may sometimes be splashed against the surface. Noseouts are the lowest activity-level aerial pattern. They are frequently seen among socializing animals, or just before or after the rest period.

3. Tail Slaps

These are loud percussive claps made by a dolphin either in normal orientation or in inverted position, slapping its tail against the water. They are sometimes given in long trains that we call "motorboating" because the resultant sound resembles that of a very slowly moving motor boat. Some of these trains last for as long as 15 seconds. Tail slaps are typical of slow moving schools.

In captivity stationary animals have been noted to tail slap. The animals simply rocked back and forth longitudinally, their tails moving up out of water as their heads moved down. Then they rocked back, and flukes were brought sharply down on the water surface.

Tail slaps occur commonly when behavior state is changing, as from rest to zigzag swimming. Single tail slaps are thought to have a signal function in many different odontocete species

ranging from sperm whales to harbor porpoises (Norris and Prescott 1961). Such slaps seem to signal danger and to initiate synchronous dives by a school. We have seen such tail slaps followed by synchronous dives in spinner dolphins, related to the intrusion of a human observer.

Clearly, though, not all tail slaps are related to signaling danger. In most cases no context is readily apparent, but they occur in slow moving schools that are not deep in a rest period.

4. Head Slaps, Back Slaps, and Side Slaps

These are patterns of moving schools, given in the direction of movement. They seem especially frequent during times of overall school acceleration in a given direction.

Viewed underwater in captivity, there seems to be no precursor behavior to such patterns. The animal swims up partly out of the water using very short amplitude strokes of its flukes. When a third to three-quarters of the animal's body is out of water it flexes, or twists and flexes so as to strike the nearest part of its body against the water with smacking sound. These sounds, in our experience, are much less intense than those generated by spins or tail slaps.

5. Salmon Leaps

An even more active form of slapping behavior is what we have come to call the salmon leap. It is seen only in rapidly moving schools. The animal leaps out of the water at about a 30-50 degree angle to the surface, and with its body held in a rather rigid arc, it falls back into the water in the direction of school movement.

The impression given by all these patterns is that they mark the direction of movement. Taken together, they give the observer a rather precise measure of the activity level of the school.

6. Spins

Spins are the patterns for which the spinner dolphin is named. They are high energy patterns often given in a series by a single animal (Figure 23). In one such sequence 14 spins in a row were counted. Spinning seems to occur at any part of a school, for our attempts to define any sector where it was most frequent, failed. It seems commonest at dusk or in the dark (judging from observations of captives) and when the school is very active and in spread formation. The spin has a well-defined precursor pattern underwater that involves both body movement and sound emission (Figure 24).

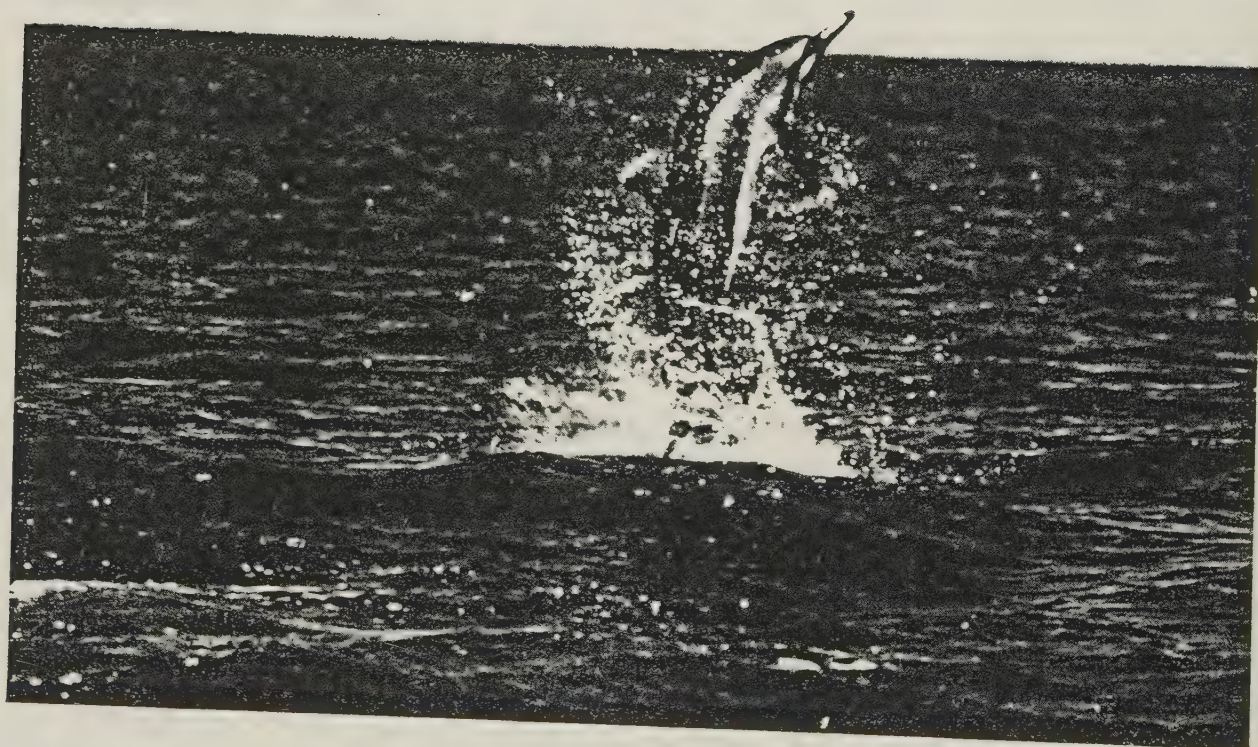


Figure 23. The spin, captured by high speed camera shutter. Spins are performed both when dolphins are in vertical orientation, as is shown here, or oriented horizontal to the water surface. Photograph by Randall Wells.

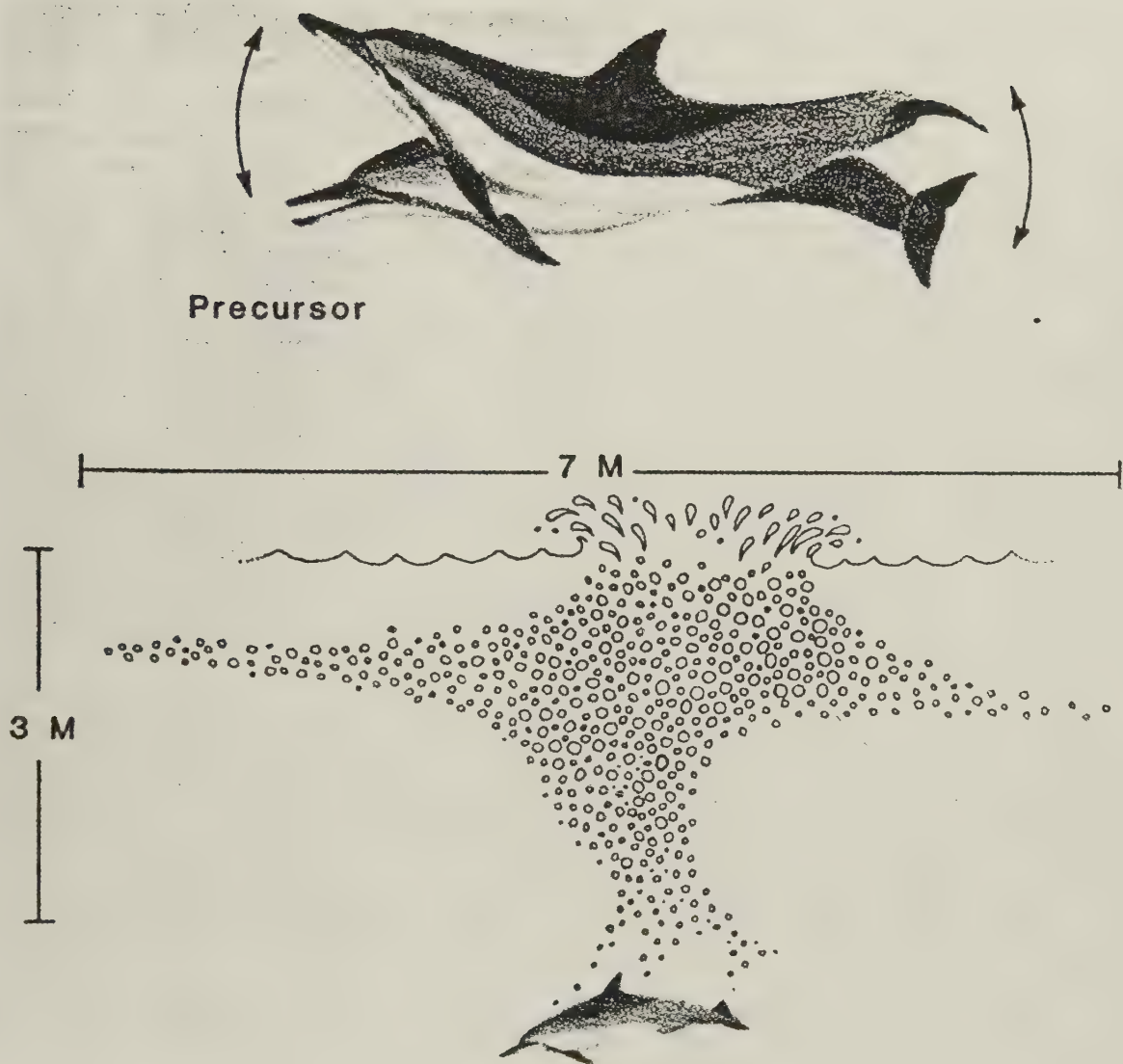


Figure 24. The spin. Top: Precursor behavior; vibration in place. The mouth is chattered and the pectoral fins sliced back and forth. Bottom: Bubble trail left by dolphin sinking after a spin. The dorsal fin contributes to the central tail of bubbles. The lateral extent of bubbles shown here is approximately the widest trail seen.

Precursor behavior, which was noted only in captive dolphins, can be subtle or quite overt. Strong precursor behavior correlates with a strong spin. Sometimes, during intense caressing sessions one partner broke away to spin, to return again to its partner. Sometimes such spins seemed to signal the termination of an association.

The animal about to spin holds its body quite rigidly in the horizontal position and bends both head and tail up and down together in a rapid and repeated body flex. At the same time rapid slicing motions are made with the pectoral fins. Sometimes these movements are given so rapidly that they become blurred vibrations, increasing in speed. None of these movements tend to propel the animal forward. If the animal is close to the bottom these movements may rub the genital region rapidly over the substrate. If the animal is in open water these jerky movements are followed by a rapid dive to 2-3 m depth, followed by swimming upward at an angle of about 70 degrees to the surface. And with ever increasing amplitude of fluke strokes until they are wide and powerful, the animal bursts through the surface. When all of the animal but the flukes and a few centimeters of the tail have left the water the flukes flash sideways at what looks to be a nearly 90 degree twist. It is suspected that this twisting is due not to the animal rotating its tail on the body axis, but to the animal throwing the air-borne portion of its body into the spin. This last moment twist seems to be a result of the spin, not its cause.

Upon reentry the animal hits the water on its back and side, rotating rapidly. A loud percussive crack of sound was usually heard at this point in the spins of captive animals. It sinks, stretched out full length. Its appendages and body draw plumes of bubbles down with it as it sinks. After the spin this plume typically drifts and may extend in length to as much as 4 m before it dissipates. Such bubbles are usually drawn downward about 2m below the surface. Such air is especially entrained by the head, flippers and dorsal fin. As many as $1\frac{3}{4}$ rotations of the animal may occur underwater after reentry, before it swims away. High energy clicks and short barks often accompany spin precursor behavior.

7. Tail-over-head Leaps

These are the most active leaps of all. They have not been observed below water and hence the occurrence of precursor behavior for this pattern remains unknown. In the tail-over-head leap the animal bursts from the water in a high arcuate leap and literally throws its tail over its head, usually accompanied by a spiraling trail of water. At the end of the leap the animal slaps the dorsal surface of its body smartly against the water, making a loud "crack", as it reenters tail first. Sometimes in very active schools animals will combine spins with tail-over-head leaps and yet contrive to make a loud slap upon reentry.

Such leaps are a bewildering melange of flashing flukes, flippers, fin and body.

8. Fluke-outs

A very passive pattern which we call a flukeout is sometimes seen in very slowly moving schools. Animals literally emerge tail first driven upward by their bouyancy, thrusting the tail stock and flukes into the air before subsiding again into the water.

9. Interpretations

Spinner dolphins are aerially active in many different ways, and our divisions are to some extent arbitrary human divisions of more variable behavior. Nonetheless our designations have allowed us to divide the occurrence of patterns clearly according to time of day (Table 2). Most aerial activity occurred in morning or afternoon, and the type shifted dramatically throughout the day. Thus deep in Kealake'akua Bay, flukeouts, noseouts and tailslaps all occurred mainly in the morning and at low frequency per animal (Table 3). These activities only bring a small part of the dolphin's body out of the water, and with the possible exception of tail slaps, are generally not very actively performed.

Those aerial activities that occurred most often per animal tended to take place in the afternoon, in our daytime records. These were tail-over-head leaps, arcuate leaps, headslaps and the various body slaps including the salmon leap. Of the various aerial patterns spins occurred with the highest overall frequency per animal, and some spins occurred on the average throughout the day. Thus, when averaged over all our records there were peaks in spin activity at 0800, 1100, and 1530, with the highest peak at 1530. Such overall averages must, however be viewed with caution because patterns such as rest may begin at different times depending upon season and time of entry into the bay, and such averages tend to mask actual relationships occurring day by day.

Spins apparently serve at least two functions. First they seem involved in signaling within the school, and second, they may serve to dislodge external ectoparasites. We did not believe this latter possibility until we examined our action-stopping still photographs of spins. Of 79 photos examined 35 showed one or more remoras attached to the spinning animal. Since remoras were not commonly seen on spinner dolphins underwater we believe they do not occur with nearly this high a frequency in the population as a whole. But we can only conjecture that the spin or the subsequent fall back into the water may sometimes dislodge remoras. A similar high incidence of remoras attached to leaping bottlenose dolphins has been noted by one of us (Wells).

Table 4. Mean position, mean radius of travel, and aerial activity per hour, of dolphins entering, resting, leaving Kealake'akua Bay, for two sample days. The positions listed in column 3 refer to X and Y coordinates of Figure 21 and 22, with X = 0, Y = 0 at the lower left of figures, and X = 2000, Y = 0 (our transit site) at the lower right.

<u>Time of day</u>	<u>Sample Size</u>	<u>Mean X & Y Positions</u>	<u>Mean Distance Traveled (m)</u>	<u>SD</u>	<u>Count of Aerial Activity</u>
July 30, 1979					
6- 7	18	1574, 932	414.1	132.42	0
7- 8	23	1950, 440	68.7	29.02	3
8- 9	37	1994, 497	138.1	66.23	27
9-10	34	1951, 547	77.3	39.33	6
10-11	26	1918, 482	53.6	27.59	4
11-12	20	1972, 595	77.4	37.68	0
12-13	21	1955, 541	78.2	42.59	0
13-14	31	1930, 938	165.3	115.34	20
14-15	6	1910, 1868	386.4	290.30	44
February 2, 1980					
9-10	9	1949, 519	92.2	46.83	0
10-11	32	1937, 531	183.5	92.19	24
11-12	21	1957, 537	125.5	48.64	3
12-13	11	2115, 848	164.9	95.74	27
13-14	37	2147, 952	65.9	35.02	8
14-15	22	2135, 853	71.9	73.56	0
15-16	38	1249, 585	383.8	226.83	0
16-17	19	1942, 1080	688.7	641.89	20

But, spinning could not always be involved with such ectoparasite removal because captive spinner dolphins regularly spin with no fish in attendance, and clearly many spinner dolphins at sea spin when such fish are not present. Spins occur in recognizable and repeated diurnal patterns which would not be expected if only ectoparasite removal was involved.

As spinner dolphins arouse from rest, their speed of travel increases, and they also begin to wander widely from their preferred rest location. In order to test the relationship between speed of movement and level of aerial activity we compared the amount of aerial activity per hour with the amount of meandering around the average location of that hour (Table 4). We found, for two sample days, a significant correlation between aerial activity and increased movement; active dolphins exhibiting frequent aerial patterns cover more territory than when they are quiescent.

Active groups usually have some dolphins at the surface and some below at the same time. Their diving tends to be asynchronous. But this changes to synchronous diving by the whole school during quiescence.

If one considers the total daily pattern of Hawaiian spinner dolphins it becomes logical to call much of the daytime occupancy of shallow protected water "rest".

They feed actively at night, on scattering layer organisms probably available only then. They move constantly and dive to considerable depths. The latter behavior is attested to by mesopelagic food items found in stomach contents in animals caught early in the day and its absence from stomachs of animals taken later in the day (Norris and Dohl 1980). Feeding schools move long distances in the dark, moving laterally along the coast line, back and forth along the island slope. Activity declines as animals enter shallow areas during the morning, whether measured by aerial behavior, swimming speed, or level of acoustic emission (Figures 25, 26). Social patterns become less and less obvious during this descent into rest, until the school as a whole often becomes a cohesive reactive unit not unlike a fish school; virtually silent and slow-moving. We have not seen these resting animals with closed eyes, hence we avoid the term "sleep" for the behavior (Figure 27).

Aerial patterns, except those used in high speed locomotion, all produce sounds at specific points in their performance, and involve a high level of coordination in doing so. They are also clearly graded by activity level. It seems logical that they should be involved in acoustic signaling within the school in relation to activity level.

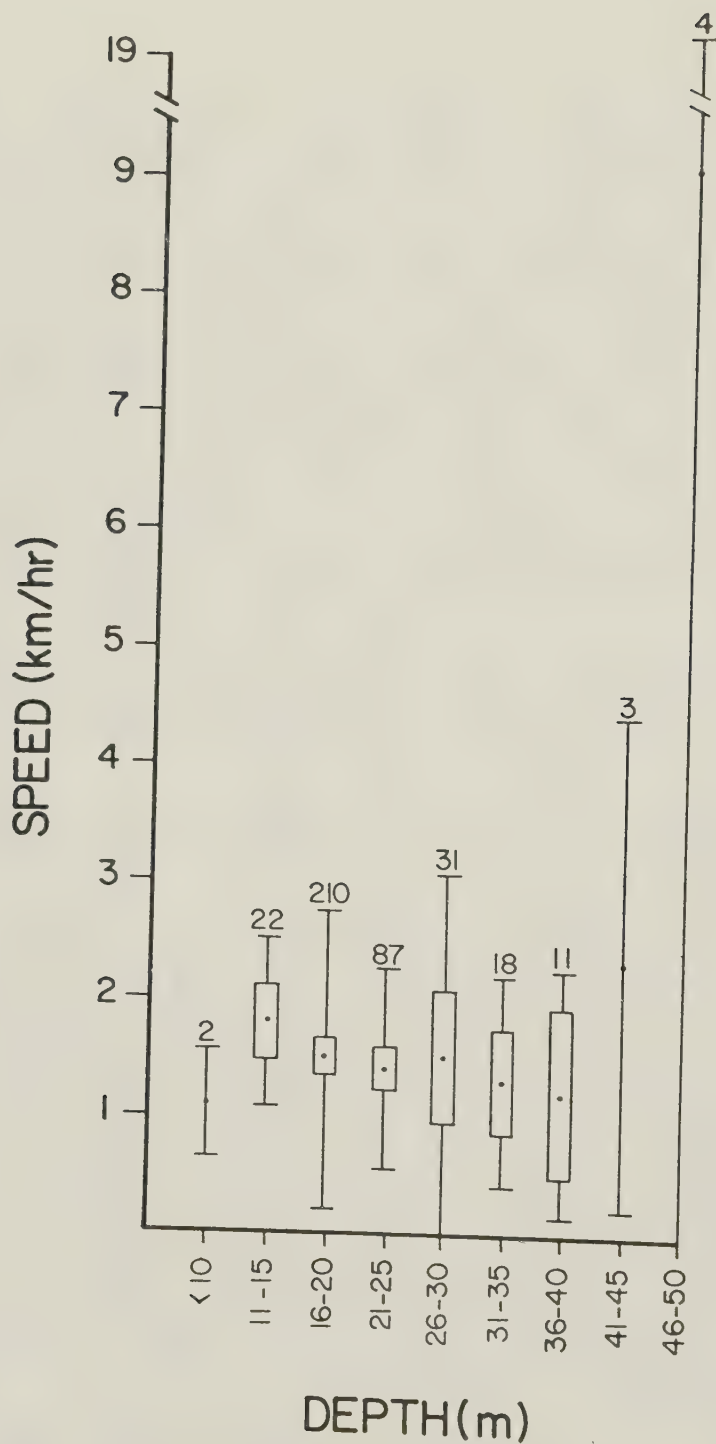


Figure 25. Average travel speed at different water depths for aerially inactive schools in Kealake'akua Bay, as determined by theodolite tracking. Bars represent standard deviations and boxes 95% confidence intervals.

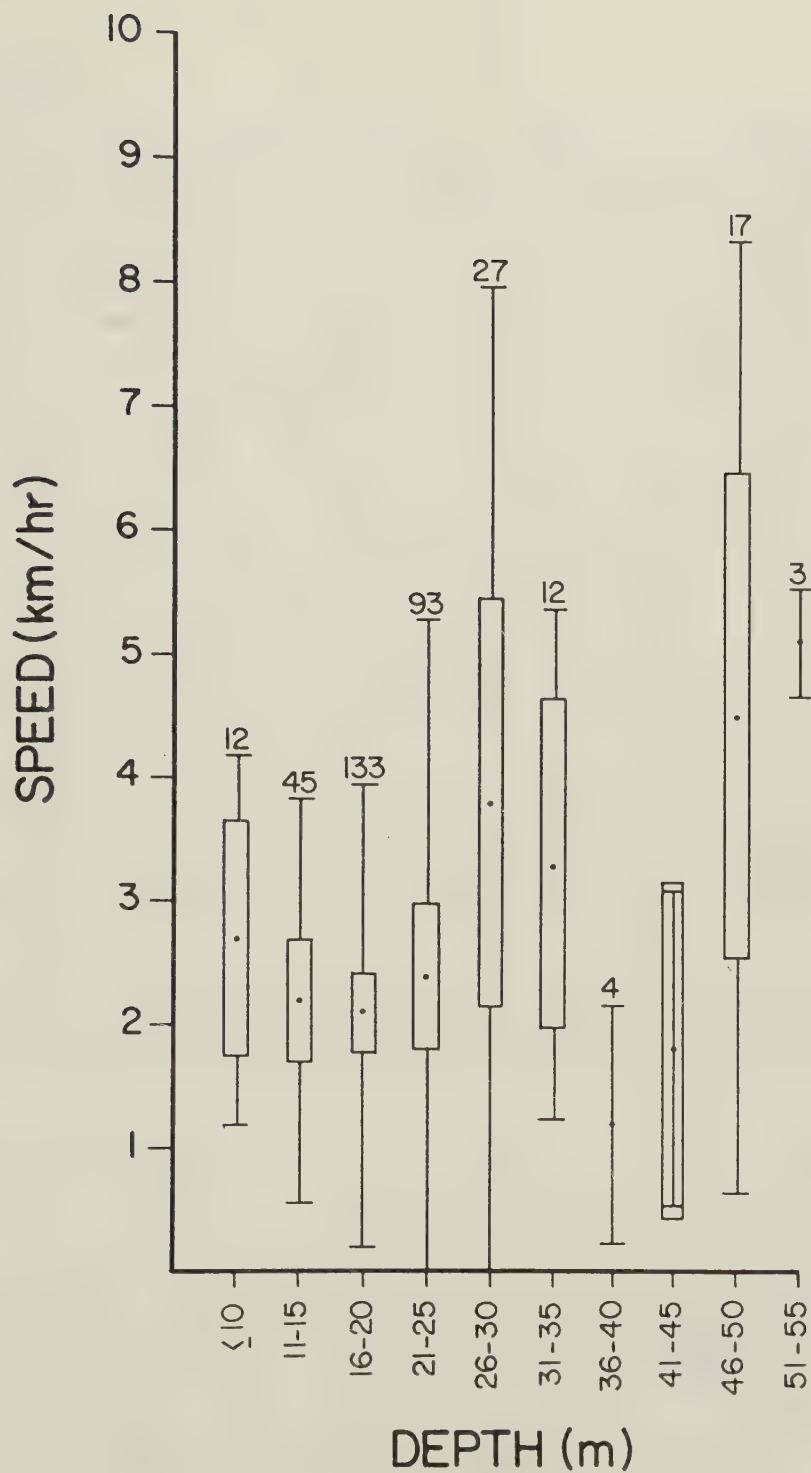


Figure 26. Average travel speed at different water depths for aerially active schools in Kealake'akua Bay, as determined by theodolite tracking. Bars represent standard deviations and boxes 95% confidence intervals.

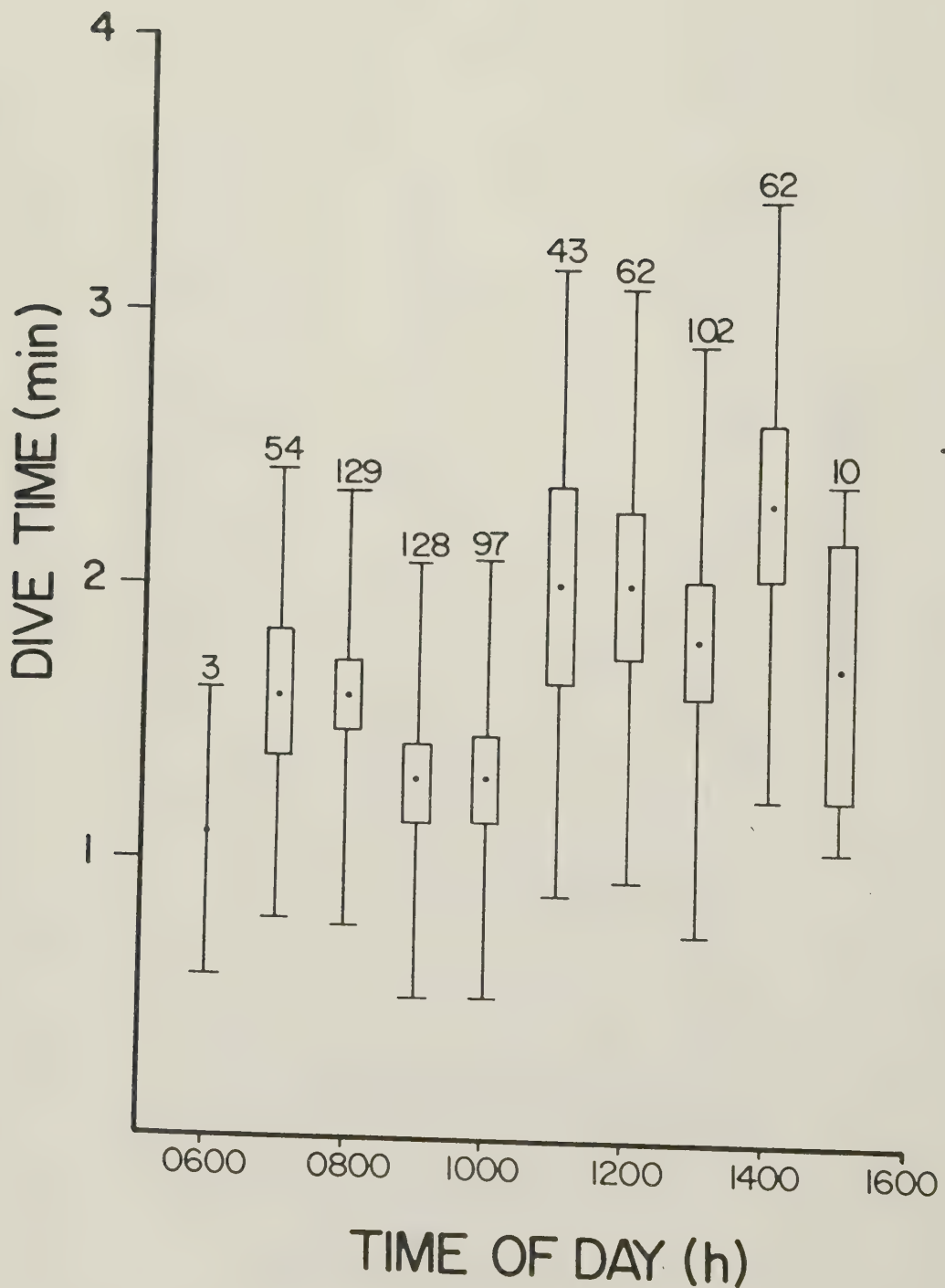


Figure 27. Average dive durations by time of day, as determined by theodolite tracking in Kealake'akua Bay. Bars represent standard deviations and boxes 95% confidence intervals.

Zig-Zag Swimming

Zig-zag swimming, which follows the rest period, consists of a period of very variable duration in which the school shows great changes in the speed and direction of movement. A usual pattern is for a waking school to begin to move out of the rest bay. Then, after several hundred meters of travel, often with many animals engaged in high-energy aerial behavior, the speed reduces, aerial behavior subsides, and the animals may begin to mill. Then they may turn and make their way back into the bay again, sometimes completely back to the rest area, and sometimes into subsidiary areas where they mill quietly. Then, as suddenly as before, aerial behavior may increase in frequency as the animals begin another sortie toward the bay mouth. This pattern continues, back and forth, usually until toward dusk, and often toward the setting sun an especially high energy sortie begins, with animals leaping high. Their course may become a direct one out to sea with all animals moving very swiftly. Especially if the pattern begins early in the day the school may also travel along the shore for a time, and then edge out to sea. Once over deep water (often about 100 fathoms) the school may abruptly spread.

In rest areas such as that near Keahole Point, where deep water is close offshore, zig-zag swimming is stretched out along the shoreline, with schools changing course many times back and forth, but with relatively little offshore movement until the last burst out to sea.

After zig-zag swimming is complete the dolphins move rapidly and resolutely offshore, and when over relatively deep water near dusk, they abruptly go into what we term spread formation.

1. Interpretation

A synthetic model for zig-zag swimming suggests that it is a period of social facilitation during which all parts of the school become alert and ready to move offshore to the feeding grounds. By this we suggest that it is a group process that can operate without unitary school leadership. The school as a whole tests its own integrity as an alert unit capable of functioning in relative safety in deep water. The features which contribute to this interpretation are these. First, zig-zag swimming follows rest and it is transitional between a quiescent period and active feeding offshore. Second, it contains a series of transitions within it; locomotion fluctuates greatly both in direction and speed, as the school oscillates back and forth between patterns like those of the rest period just past, and those of the feeding period just ahead. The animals move back and forth between places of rest and future activity. Acoustic behavior is also oscillatory. Resting animals are singularly quiet, emitting only sporadic low-level clicks and very occasional whistles.

Burst-pulsed signals are all but absent during rest. Such oscillation in acoustic emission frequency continues throughout zig-zag swimming and builds to a crescendo of sounds that include, seemingly, choruses of whistles from every animal, barks, and showers of clicks until a maximum is reached in the last sortie and the animals finally make their high-activity dash out to sea.

An experimental study of whistle emission and chorusing by the closely related genus Delphinus (Caldwell and Caldwell 1968) may be related to such social facilitation. Whistle choruses between two animals were found to be related to the timing of whistle initiation. If one animal whistled and the second responded 0.7-0.8 seconds after the first, the first animal would continue whistling and the two would chorus. If the response of the second animal to the first was too rapid or too slow, the first animal fell silent.

If our spinners are responding like Caldwell's Delphinus, whistle choruses during zig-zag swimming could be an acoustic means by which one animal tests the alertness of another. Our choruses of whistles, given as the dolphins start their dash out to sea, are times when acoustic unanimity as an indication of alertness is expressed. Such simultaneity could be a prerequisite to such offshore movement where predatory sharks have an additional degree of freedom in their movements because the dolphins have entered deep water.

Spread Formation

The preliminary study of Norris and Dohl (1980) did not recognize this very distinctive part of the diurnal pattern. After zig-zag swimming is complete the animals quickly enter a high speed swimming period oriented sharply offshore, which is typified by much aerial behavior, especially such directional patterns as head and back slaps and salmon leaps. This travel is so resolute and rapid that an observer has to be very alert and ready to travel or the animals will simply be lost in a few moments, and out of sight. As the water deepens, the traveling school, which has become a swiftly moving column or rank of animals, suddenly stops, and small subgroups disperse in many directions. These subgroups, sometimes including fairly isolated adults and young, may quickly spread over kilometers of sea. The observer attempting to follow the school may look up in bewilderment, wondering where the school went. Parts have gone in all directions, and from the surface, not all can be seen from a single location.

1. Interpretation

The function of spread formation is not securely understood, but it occurs near dusk when the dolphins are presumably locating

food sources, and before they aggregate into coherent feeding schools. By such spreading a quite rapid assessment of local abundance of food could be made, with animals later coalescing on that source, and reforming as a feeding school.

That this is an active formation is indicated by the high sound emission level typical of spread formation, especially of whistles, which as we postulate later may be the major means for assuring school coherence when animals are widely separated, or when darkness reduces the effectiveness of vision.

Movements along the Kona Coast

While following dolphin schools offshore until dusk provided much information on offshore movements and the behavior of spread schools, radiotracking proved to be the only effective means of keeping track of individuals or schools in the dark, and continuously for several days. Four dolphins were captured for such tracking. The first animal did not receive a radio transmitter but was equipped with visual tags. It was reported 34 days after tagging in a group of 100-150 spinner dolphins off the North Kohala coast, between Kawaihae and Upolu Point (Figure 28). This is the northernmost sighting of any of our identifiable animals. Two weeks later it was resighted in Kealahou Bay. On both occasions its radio tag and freeze brands were clearly visible.

The following three animals were radiotagged. None of the radiotags lived up to our expectations but much information was gathered during their relatively short lifespans. The radios transmitted to 1.3, 6, and 1.5 days, respectively (Table 1). Though the small size of these transmitter packages relative to those we have used previously (Würsig 1976, Irvine et al 1981, Norris and Dohl 1980) was no doubt advantageous in terms of reduced drag, the packages suffered from short range.

Radiotagged dolphin #1 (RT-1), a female captured off Wawahiwa on October 25, 1979, quickly rejoined her school following release at 10:05 as it headed steadily south (Figure 29). The school of about 100 animals milled near the mooring area at the port of Kailua. The school also contained the naturally marked dolphin "Four Nip". The school was quite scattered until it headed south in a slow zig-zag pattern at 11:45. At 12:30 the level of aerial activity began to increase. This was followed by a general movement offshore from Kahaluu. The school began traveling rapidly north at 16:24, approximately over the 100 fathom contour. At Honokohau they headed offshore once again, swimming quite rapidly with much aerial activity. Following a crew change we followed RT-1 to about 9 km off Makalawena at 19:25 where we lost the signal and returned to shore because of building seas.

The animal was relocated at 08:06 on October 26, in a very active school of about 80 animals, headed south from Hoona Bay.

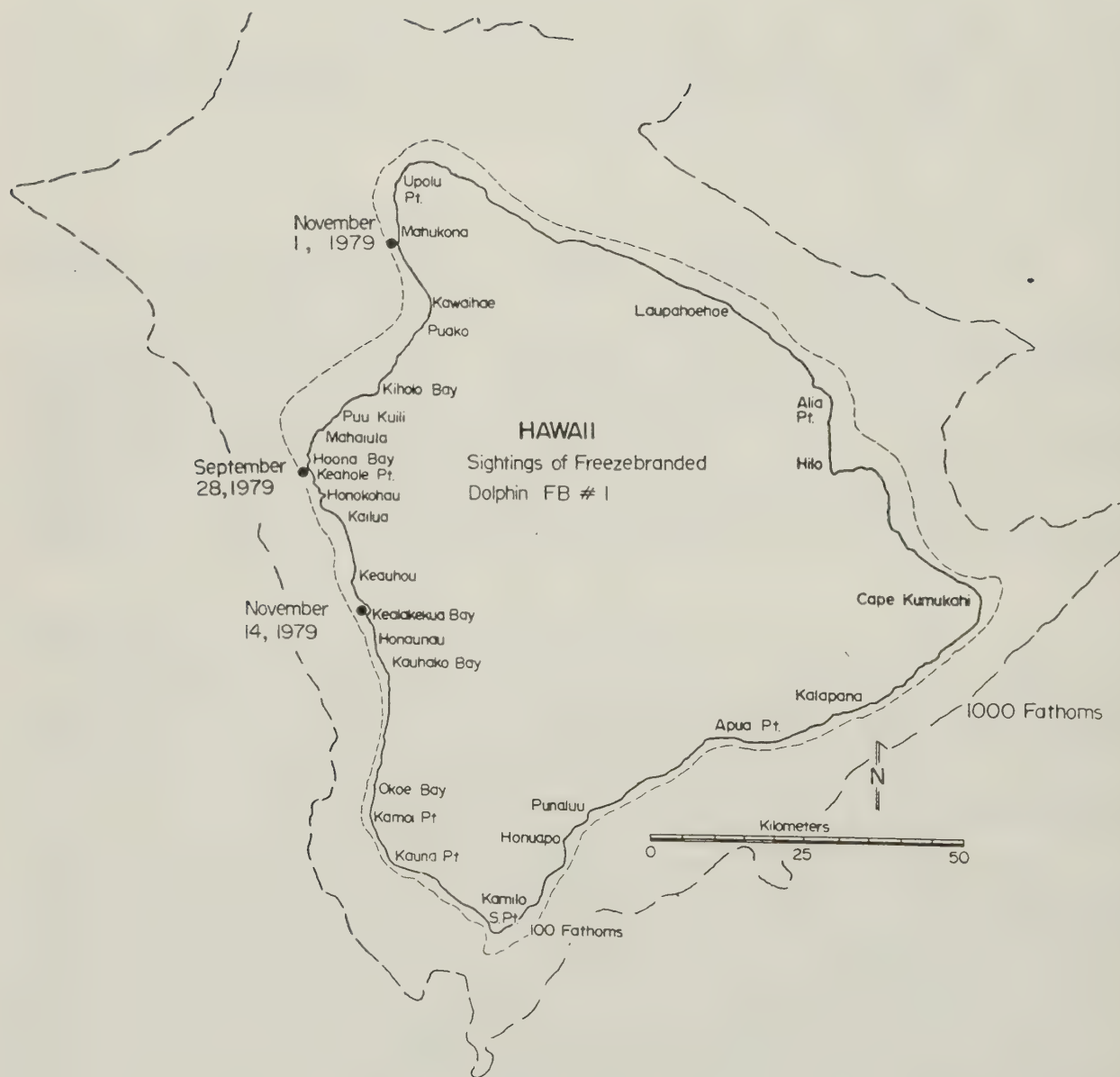


Figure 28. Sightings of marked spinner dolphin, FB-1, captured September 28, 1979. The November 1st sighting was reported to us. The November 14 sighting was with radiotagged dolphin RT-2.

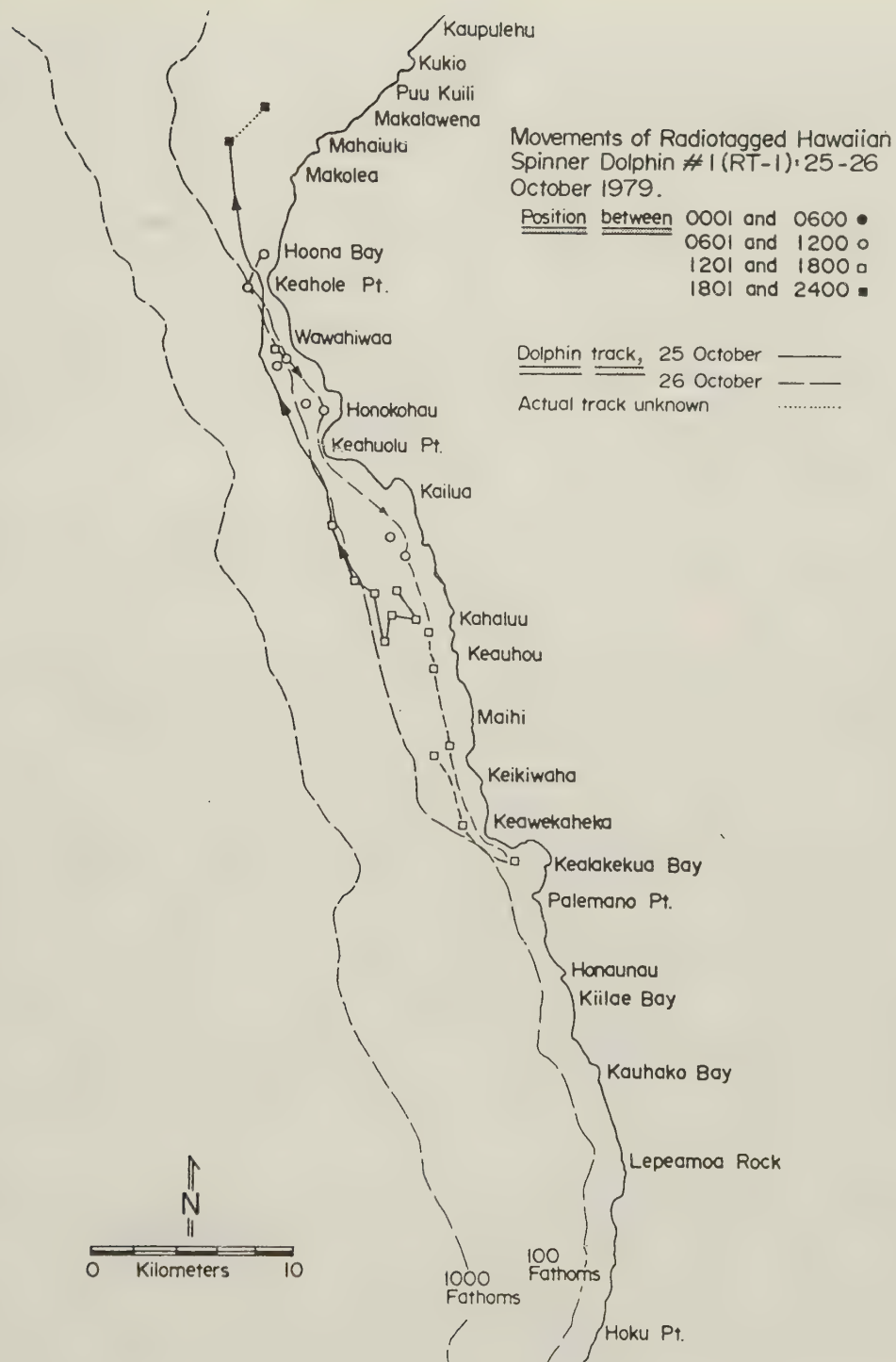


Figure 29. The movements of radiotagged spinner dolphin RT-1, along the Kona Coast of Hawaii.

All size classes were evident in the school. By 10:52 the school was headed south through Kailua Bay. They continued moving steadily south, nearshore, passing Keauhou at 12:20 until they reach Keikiwaha Point where they milled briefly and then continued south. At 14:46 the school entered Kealake'akua Bay, where another group of 30 dolphins including the naturally marked animal "Finger Dorsal" had spent much of the day. Four Nip was seen for the first time when these schools met at 14:52. All the animals headed out of the bay together amidst much acoustic activity, moving steadily north parallel to shore. At 16:02 they milled north of Keikiwaha. At 16:35 the school headed due magnetic west towards the setting sun. After we lost the signal from the radiotagged animal we followed the school visually to about the 100 fathom contour where they spread, and following the contour, moved north.

Thus, this animal and its school moved more than 30 km along the shore in less than a day, and moved offshore presumably to feed, at widely separated points on the two monitored nights.

On November 1, 1979, RT-2 (a female) was captured at 08:50 in Hoona Bay from a school of 30-40 spinner dolphins and fitted with a radiotag. Following release at 09:04 the dolphin rejoined its school as it moved rapidly south near shore. The school slowed as it reached Honokohau and continued slowly into Kailua Bay where it milled in scattered subgroups (now totaling about 60 animals) until 13:05 when the dolphins moved slightly further offshore. At about 13:30 the school increased speed and turned north. By 15:35 its broad rank formation was headed west off Keahole Point. As the school reached the 100 fathom contour at 15:57, it turned to the north and spread into scattered subgroups. At the school's farthest record position from shore, at 17:00, about nine km west of Makalawena, there was greatly increased aerial activity among the close-knit subgroups that dove and surfaced in synchronous fashion. At this point we returned to Honokohau for a crew exchange. The animals were later encountered nearer shore off Makolea, and they moved south through the night.

The second radiotagged dolphin (RT-2) spent the first day and night in the northern part of the study area, but then moved south and spent the last four days south of Kealake'akua Bay. In the daytime it and the school(s) with which it associated stayed close to shore, and at night moved into deeper water. This pattern is shown in Figure 30, where only nine of the 29 (31%) daytime positions are outside of the 100 fathom depth contour, but 14 of 20 (70%) nighttime positions are in deeper water.

A school of 60-80 dolphins including RT-2 entered Kealake'akua Bay at about 07:00 on November 3, 1979. The school moved slowly in rest formation through the bay until 13:30, when they left the bay to the south, in a flurry of aerial activity. By 14:35 they were over the 100 fathom curve off Honaunau, still

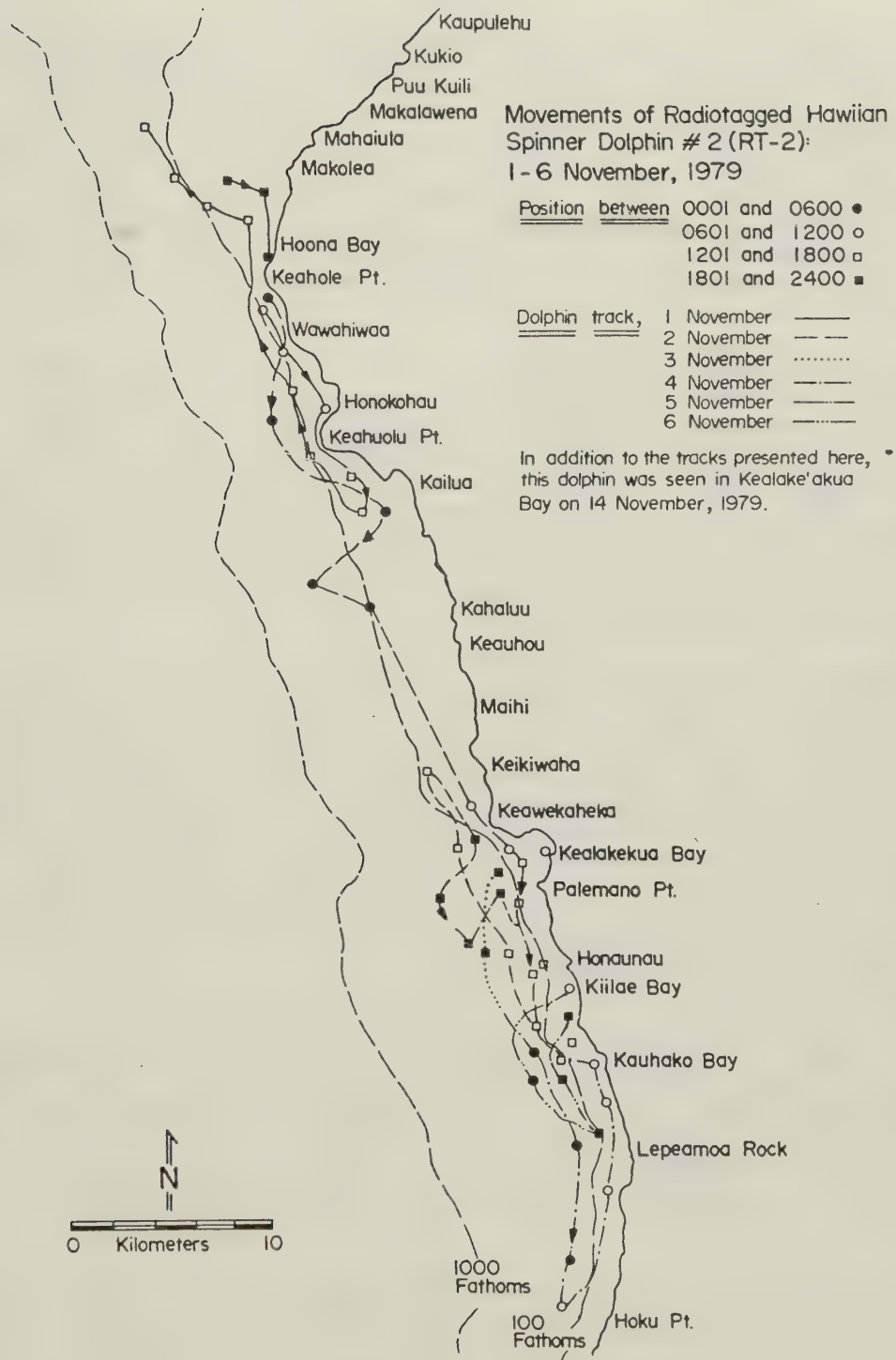


Figure 30. The movements of radiotagged spinner dolphin RT-2, along the Kona Coast of Hawaii.

headed south in scattered subgroups. The school turned to the north-northwest after moving offshore at 15:11, and continued until they were off Keikiwaha Point. There they turned south and were apparently milling about two km off Honaunau at 22:00, over about 400 fathoms of water. Based on the distance of the radiotagged animal from the boat, while we could see other animals nearby, the school as a whole must have been quite scattered. Hydrophone recordings made at this time contained abundant click trains and whistles. The vessel Nai'a returned to Kealake'akua bay at 24:00.

The dolphin RT-2 was found from the air on November 3, 1979, at 12:47 swimming nearshore just north of Kauhako Bay, in a school of over 60 individuals. The animal was located later by boat off the southern point of Kealake'akua Bay at 22:00, engaged in long dives, about 0.5 km from its position of the night before at the same time. Signal strength was declining and could only be heard 1.5 km from the animal. The animal was tracked to the south. It was off Honaunau at 23:44, and far to the south, only nine km north of Milolii by 03:40 on November 4, 1979, when the school turned north again.

A rapidly swimming file of about 60 dolphins including RT-2, Finger Dorsal and Four-Nip, was encountered several km south of Kauhako Bay at 06:05, headed north in a close-knit school near shore. By 07:50 they had spread into a number of subgroups. About half of these animals entered Kauhako Bay at 08:32, while the remaining animals milled about 1 km to the south. This trailing school included RT-2 and Finger Dorsal and was met offshore of the bay at 10:22 by the earlier arrivals. Following milling and mixing of the main subgroups the first school apparently moved northward while RT-2 and associates milled in Kauhako Bay for much of the day.

The activities of RT-2 were concentrated in the southern part of the study area for the remainder of November 5. On November 6, the animal entered Kealake'akua Bay, and the signal weakened and was lost. On November 14, RT-2 was sighted in Kealake'akua Bay with FB#1 (the marked animal without a radio transmitter). Dolphin RT-2 still had the transmitter on its fin but one of the mounting bolts was missing. It was not sighted again.

Dolphin RT-3, a male, was captured from a school of about 35 animals off Kahaluu, on April 26, 1980 (Figure 31). He rejoined his school at 10:44, as they swam about 2 km north of Kahaluu. At 11:16 the school headed south near shore. We broke off observations at 12:56 to refuel at Honokohau when the animals were in Maihi Bay. Part of the school headed due magnetic west at 16:35, but a subgroup containing RT-3 remained in Maihi Bay, milling and surfing on the swell. At 17:18 Nai'a put into Keauhou to attempt repairs. The dolphin was relocated at 23:03 2.2 km southwest of the Cook Point light, heading inshore and to the

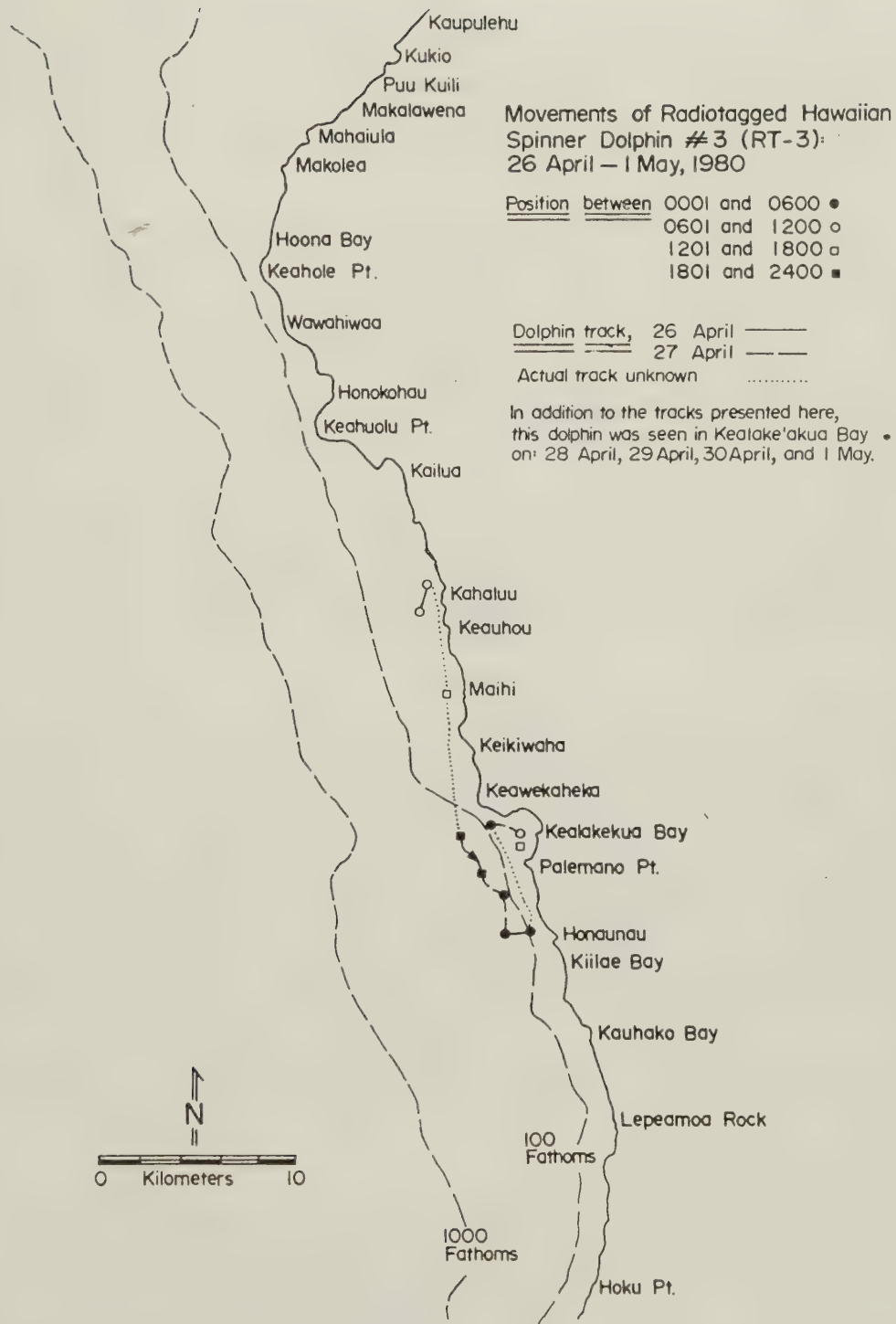


Figure 31. The movements of radiotagged spinner dolphin RT-3, along the Kona Coast of Hawaii.

south. The tagged dolphin was near the 100 fathom contour off Honaunau at 02:32 on April 27, and then it turned inshore and headed north. The radio signal deteriorated and was temporarily lost at 04:15. At 05:33 a school of dolphins was sighted off Keawekaheka Point, headed toward Kealake'akua Bay, and we received a poor signal. By 06:26 the school of about 50 dolphins was located just north of the mooring area in Kealake'akua Bay. The school included RT-3 as well as calves and animals with tall erect dorsal fins. We moored at 07:00 and monitored the school from shore until 12:00. The school left Kealake'akua Bay at about 10:00 only to return at about noon. The dolphin RT-3 was sighted with one of the two main subgroups at 1220 milling quietly. The school left Kealake'akua Bay at 18:27, passing Keawekaheka Point, moving north. The signal was lost and no further signals were received by Nai'a, or the InterAmerican Tropical Tuna Commission station on the ketch Nelly Bly, or from the mobile shore station.

On April 28, 1980, RT-3 was seen again in Kealake'akua Bay in a school of about 50 dolphins. There was no signal and the antenna was seen to be missing from the animal's radio. On April 29, the dolphin was seen again in Kealake'akua Bay with about 80 dolphins, and again on May 1 in Kealake'akua Bay with from 80-100 animals.

At no time was RT-3 an obvious part of school subgroups. It was generally farther from its nearest neighbor than were other dolphins, and was not noted swimming synchronously with other animals, even though most other school members were in pairs or trios much of the time. However, its respiration rates appeared to match those of other schoolmates, as determined from the theodolite station. This phenomenon of remaining near but not being an actual part of the school subgroups was observed for all three radiotagged animals, and similar behavior has been noted by Irvine, Wells and Scott (1982) for some radiotagged bottlenose dolphins, and by Würsig (1976) for dusky dolphins. Recent work by one of us (Würsig) with extremely small radio tags on dusky dolphins indicates that such separation is not present when the tag does not appear to hamper the movements of the dolphin.

1. Interpretations

These radiotracking records showed larger scale daily movements than we expected, but even so they do not define the limits of the ranges of individual dolphins as we know from scars and marks analysis, which show the same animal in both Kona and the Hilo area. And although these dolphin school sightings were all concentrated along the Kona coast between about Kaupulehu and Kauhako Bay, spinner dolphins have been sighted along the entire coast of the Big Island during our aerial surveys. They also have been reported well offshore (Wayne Perryman, NOAA, personal communication).

Dolphin FB#1 was sighted along about 95 km of coast, between Kealake'akua Bay and approximately Mahukona. But even though dolphins range widely, our records also carry hints that there may be more local areas within which the activities of certain dolphins are largely concentrated. Excursions outside the central Kona coast may be the exception for many animals, rather than the rule.

But sighting data must be considered in the light of sighting effort. Only one boat survey was made in waters north of Kiholo Bay, and no spinners were sighted. And only one boat survey other than radiotracking went more than a few kilometers south of Kauhako Bay. Therefore, though the regions of greatest dolphin concentration were monitored fairly extensively it cannot be said that any of our marked animals ranged outside the study area. But, several distinctively marked dolphins were seen much less frequently than would have been expected if they occupied only the central Kona coast. At best we can say that some spinner dolphins along the central Kona coast seem to concentrate much of their activity within reasonably localized sections of this coast. It is possible that this coastal population is composed of a mosaic of overlapping ranges of different populations or individuals.

The patterns of daily movements for the three radiotagged dolphins were quite similar in several respects. Daytime movements were generally inshore, with animals moving slowly north or south along the coast, often reversing course sometime during the day. Or the dolphins moved along the coast until they encountered a bay such as Hoona, Kealake'akua, or Kauhako in which they milled for prolonged periods. During the afternoon the animals moved offshore, often due magnetic west, toward the setting sun, usually as far as the drop-off of the island slope at between 100 and 1000 fathoms depth. At night they tended to move along the coast more or less in this same depth area. Figures 32, 33, and 34 depict the relationships between time of day, water depth, and distance from shore for the three radiotagged animals.

When using bays the animals tended to enter them near sunrise and leave well before sunset. The largest offshore excursions and the passages through waters of greatest depth consistently occur in the evening hours. But the dolphins did not remain in the deep offshore waters continuously throughout the night. Instead their movements passed back and forth over deep water escarpments at times and then back into shallower inshore waters as they moved roughly paralleling the coast.

Judging from both radiotracking and marked animal data dolphins appeared to concentrate their activities in particular regions of the coast for periods of several days before moving to another section of the coast where the pattern was more-or-less repeated. Movements within an area were roughly repetitive with a given dolphin starting in a specific bay and often returning to

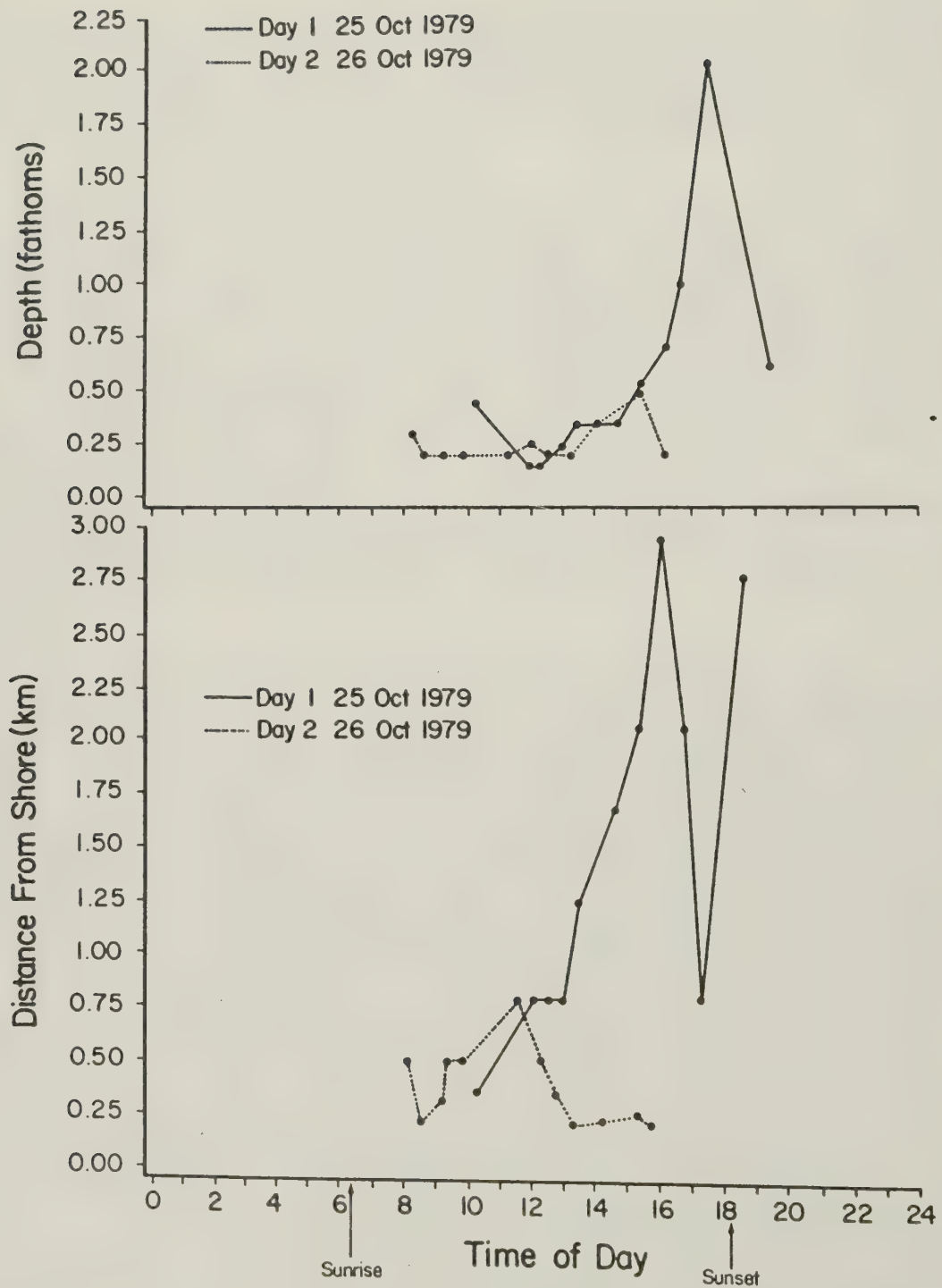


Figure 32. Movements of radiotagged spinner dolphin RT-1 in relation to water depth, distance from shore and time of day.

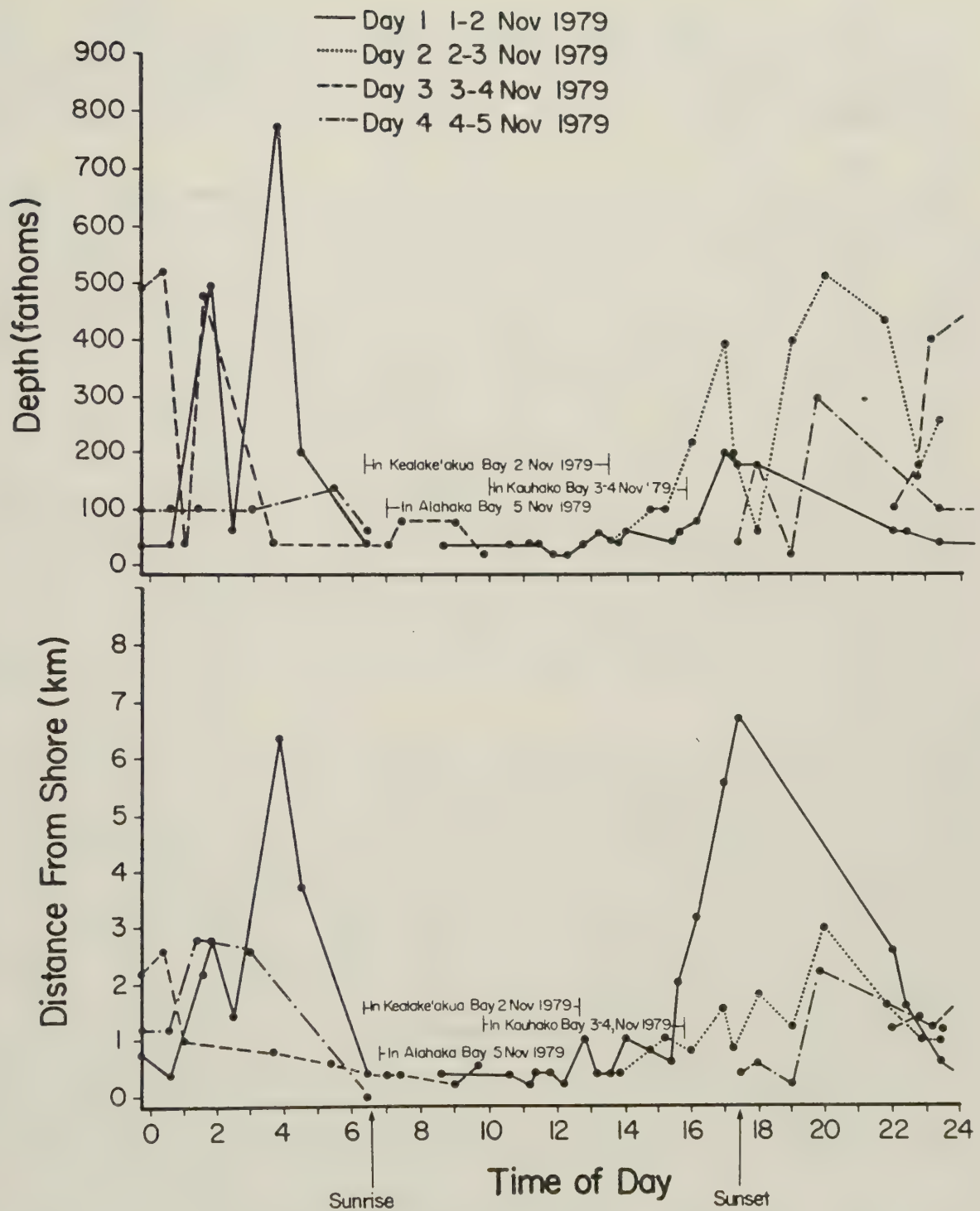


Figure 33. Movements of radiotagged spinner dolphin RT-2 in relation to water depth, distance from shore and time of day.

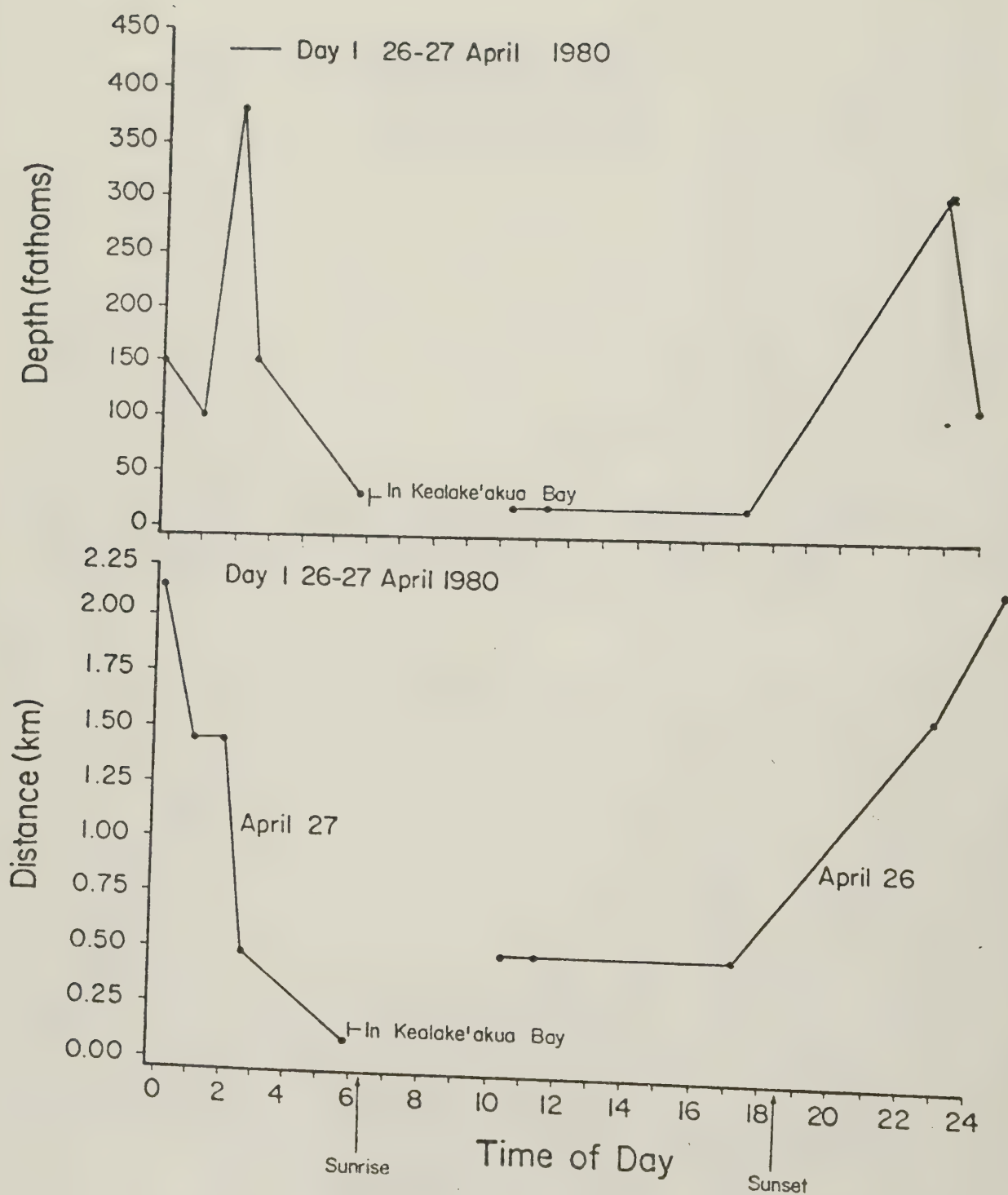


Figure 34. Movements of radiotagged spinner dolphin RT-3 in relation to water depth, distance from shore and time of day.

it the next day. Dolphin RT-2 provided a good example of this pattern. It was found within 0.5 km of the location of the previous evening at the same time on November 3, 1979. Similar repetition of movement patterns has been reported for bottlenose dolphins in the Gulf of Mexico (Irvine, Scott, Wells and Kaufmann 1981).

One striking feature of the tagging study was the high level of school and subgroup fluidity. The radiotracked dolphins clearly associated with different individuals from day to day.

Of 20 identifiable dolphins with which RT-1 was seen on October 25-26, 1979, only two were seen in the same group on both days (#70 and #101, Figure 35). In total seven identifiable dolphins were seen repeatedly with RT-2 between November 1-14, 1979, including four that were resighted with RT-2 with one or more days intervening between sightings (#11, #24, #69, and #93, Figure 36). Twenty-eight identifiable dolphins were recognized with RT-3 from April 27-30, 1980, but only four of these were seen in the same school with RT-3 on consecutive days (#61, #69, #169, and #170; Figure 37). Though the lack of consecutive sightings might be partly a function of not completely photographing each school, considerable effort was made to photograph all animals. Several of the marked dolphins that were not reidentified were among the most distinctive animals in our catalogue, and it is unlikely that they would not have been identified either by eye or from photographs. In addition, school sizes varied considerably from day to day.

Schools containing radiotagged dolphins were observed to change composition. For example, RT-1's school swam south to Kealake'akua Bay in the late afternoon of October 26, 1979, and met a school already in the bay. The schools merged and left the bay together shortly thereafter, and after moving north as far as Maihi Bay, headed offshore. On November 4, 1979, a school consisting of several large subgroups moved north along the coast south of Kauhako Bay. Two schools entered Kauhako Bay early in the morning while another (containing RT-2) moved to the south. As RT-3's school entered the bay, the first two schools left to the north. Schools also seem to change composition during the night while animals are moving along the coast in large widely scattered schools. This would account for changes in school composition from day to day when "joinings or splittings" were not observed. These examples of fluidity of school composition match those determined from records of naturally marked dolphins, and with the observations of Norris and Dohl (1980).

A final feature of importance came from this part of our study. Our catalogue of animals identified by scars and marks has pieced together a picture of movements of individual animals, and school mixing, but it also indicated that perhaps five times as many dolphins frequent the coast as we usually see from flights along the coastal resting bays. This puzzling

<u>Dolphin #</u>	<u>25 October</u>	<u>26 October</u>
01		X
02	X	
09		X
13		X
45	X	
51		X
68	X	
70	X	X
77	X	
101	X	X
102	X	
107		X
116	X	
119	X	
122		X
123		X
124		X
128		X
179		X

Figure 35. Associations of radiotagged spinner dolphin RT-1 with other identified dolphins. Identified dolphins are listed in left hand column, and days on which they were seen in the school with radiotagged dolphin are indicated in other two columns. Associated animals seen both days are connected by solid lines.

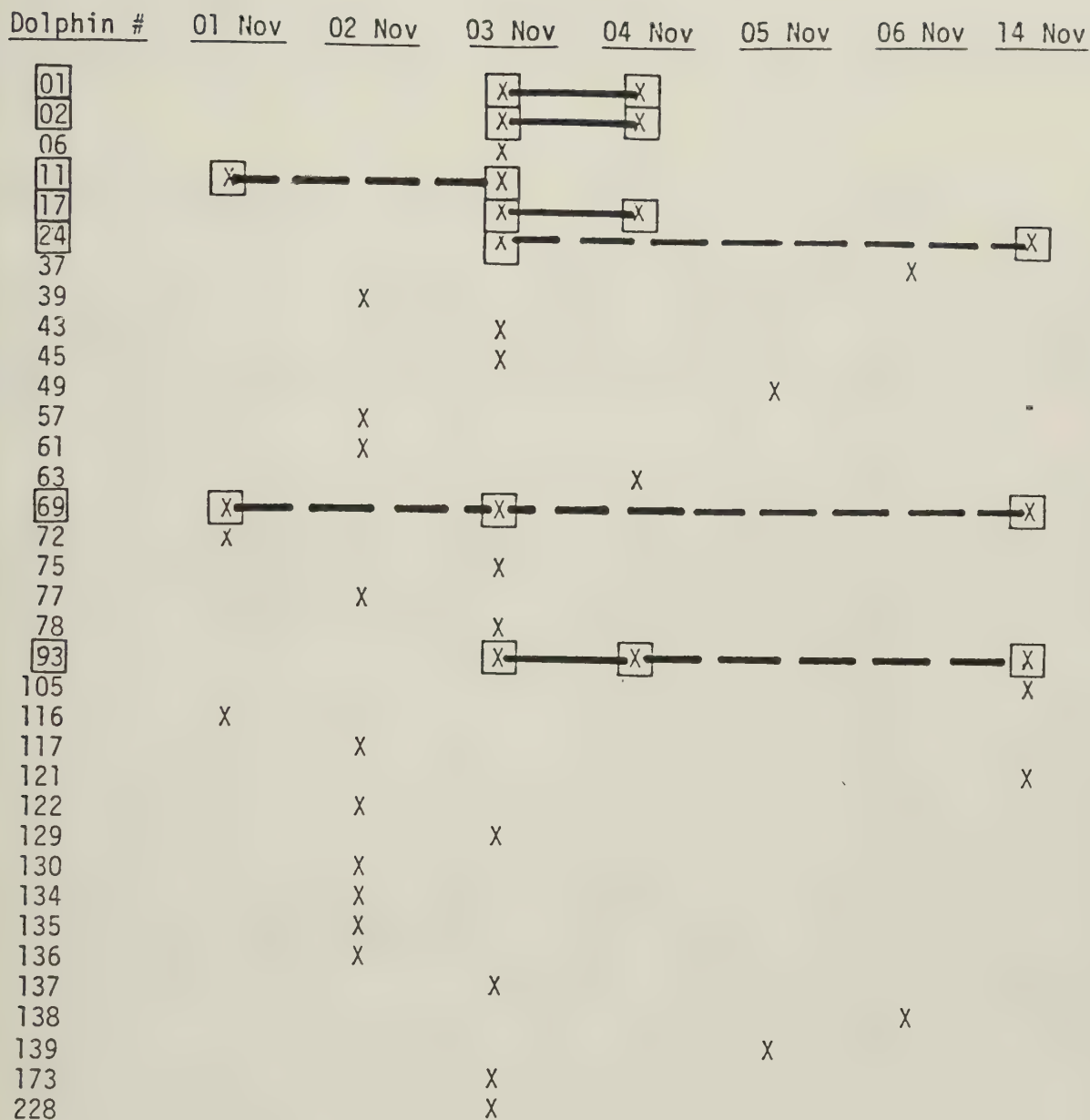


Figure 36. Associations of radiotagged spinner dolphin RT-2 with other identified dolphins. Identified dolphins are listed in left column, and days on which they were seen in the school with radiotagged dolphin are indicated in the other two columns. Associated animals seen together on consecutive days are connected with solid lines, non-consecutive days are connected with dashed lines.

<u>Dolphin #</u>	<u>27 April</u>	<u>28 April</u>	<u>30 April</u>
02		X	
03		X	
06		X	
11		X	
17		X	
24		X	
26		X	
43		X	
49		X	
52	X		
61		X	X
63		X	
69		X	X
74		X	
94		X	
129		X	
145			X
151		X	
153		X	
164		X	
166		X	
167		X	
169		X	X
170		X	X
172		X	
173		X	
174		X	

Figure 37. Associations of radiotagged spinner dolphin RT-3 with other identified dolphins. Identified dolphins are listed in left hand column, and days on which they were seen in the school with the radiotagged dolphins are indicated in the other two columns. Associated animals seen together on consecutive days are connected by a solid line.

result may now be resolved because our radiotracking data show that not all animals occupying the Hawaiian coast go every day into rest coves. Some seem simply to travel a modest distance offshore during the day, following the diurnal pattern of daytime rest.

Acoustic Studies

This section is primarily an attempt to match the frequency of emission of various classes of sounds to behavioral state throughout a day's activity. Because we know the daily sequence of behavior for spinner dolphins clearly, and because this sequence is repeated without basic change from day to day, we can match any changes in sound emission to behavioral events in this wild species.

Other attempts of this sort with delphinids have usually suffered because the listener did not know the context of behavior with clarity. At this writing only the work of Tyack (1976) on Argentinian Tursiops schools and Ford (1984) on killer whale schools appears to have developed correlations of daily cycles of sound emission and definable behavior patterns to a degree that allows relatively fine-grained analysis.

But this is only half of what one must achieve to develop meaningful correlations. If one seeks changes in the frequency of sound emissions per animal, one must estimate the number of phonating animals present for each such attempted correlation. This estimate is fraught with difficulty. To produce a useful estimate, each time we recorded we estimated the school size by eye, and then made a running commentary into a hand-held cassette recorder of the movements, headings and distances of animals from the hydrophone as the acoustic recording was being made. This let us select segments of the tapes in which the preponderance of animals moved toward the hydrophone and were within listening distance. Undoubtedly such visual estimates contain considerable error, and animals underwater may not all have faced our hydrophone. Nonetheless, very clear correlations emerged between frequency of sound emission and behavioral state (Figure 44, Table 5). This is probably as much a tribute to the magnitude of the acoustic differences between behavioral states as it is to our success at standardizing. Conversely, our ability to discriminate acoustically between clear behavioral classes waned as their similarity increased, especially if activity levels were similar. For example, our ability to discriminate acoustically between schools entering rest coves in the morning and awakening schools after the rest period was doubtful.

It is likely, we think, that new methods that allow more refined analysis than ours may well show clear acoustic differences between patterns of such similar activity level.

Since we were unable to make visual estimates of school size in the dark, our estimates were made near dusk. Schools were followed from rest in Kealake'akua Bay, through spread formation and into feeding formation. By this method we were sometimes able to travel with feeding schools and to see the subgroups silhouetted against the last light. It was then that we noted the reaggregation after spread formation and the subsynchronous diving that typifies such feeding schools.

1. Classes of Sounds

Before describing correlations we will outline the classes of sounds used in our analysis. Spinner dolphin sounds are presently indistinguishable from the sounds of other oceanic dolphins such as other species of Stenella, or Delphinus, that feed on small fishes, shrimps or squid. All emit broad band clicks, pure tone whistles, whistles with harmonic structure, screams, and various burst-pulse signals.

Burst-pulse sounds have been given many names on the basis of how they sound to the human observer; "blats", "barks", "chirps", etc (for example, see Busnel and Dziedzic 1966). We avoid setting up such classes here but note that two clear kinds of burst-pulse signals can easily be discriminated in our records on the basis of physical structure. These we call "repetition rate signals" and "multiple transient signals".

Repetition rate signals are ones in which the human listener hears the repetition rate of click trains as a frequency. Analysis will break these signals down into a very rapidly-given trains of fast rise-time clicks. Multiple transient signals are ones in which many often overlapping single transients make up a sound. These cannot be resolved into click trains.

Spinner dolphin clicks are extremely short duration rapid rise-time transients that have energy from the low audible range to at least 65 kHz, which was the upper limit of our recording system. There is probably no difference, in terms of the means of generation, between clicks and repetition rate signals, though the more slowly given clicks (to about 700 clicks/sec) are generally assigned an echolocation function while burst pulses of higher repetition rate are considered social in function. The assignment is rather gratuitous and must be viewed with reserve. Only because the slower click trains are observed in animals during exploratory behavior, and are typical of trains heard during echolocation tasks by trained animals do we call them echolocation clicks. It is not unlikely that both navigational and social meanings are involved.

Whistles are pure tone emissions, some with and some without evident harmonics, and some that grade between the two states. Typically they last from 0.1 to 1.5 seconds, though most are near

0.7 seconds duration. Whistles generally sweep up in frequency (61% sweep up).

Screams are narrow band signals that none-the-less cannot be classed as pure tone signals because a discernable bandwidth of about 1 kHz can be seen.

Burst-pulse signals are the most complex spinner dolphin sounds, spectrally speaking. They last from 0.2 to about 4.0 seconds with a mean of 0.5 seconds with energy from the low audible to the upper limit of our system, although most fall between 5-60 kHz. A number of merging classes of these signals could be erected based on their sound to the human listener, but because our waterfall display apparatus does not allow reliable resolution of clicks (its scan rate is frequently slower than the rate of click emission, and because clicks are very brief they are often missed altogether) we cannot seek a physical basis for these differences and make no such attempt here.

Analysis of whistles, on the other hand, is direct with the waterfall display. As has proved true in other studies (see Taruski 1979) attempts to divide whistles into discrete categories begin to fail as sample size increases. The boundaries between such human-erected categories begin to blur as more and more whistles enter the data base. We feel that instead of representing discrete categories with discrete meanings they are more likely parts of analogic series in which varying emotional levels relate to changes in the sounds.

2. Sounds and Behavior

The spinners emitted different numbers of sounds per animal per unit time, and a differing balance of sound classes during different behavior periods. We used discriminant analysis to show that a given behavior period could be predicted on the basis of the number of clicks, burst pulses, screams, whistles with harmonics and pure-tone whistles emitted per dolphin during five second samples. It was simple to discriminate between samples from active periods such as traveling, spread and feeding schools versus samples from more inactive periods such as entering rest bays, descent into rest, and rest periods (Figure 38).

Zig-zag swimming, which follows the rest period, was not typified statistically because of the small sample and because the frequency with which various classes of sound occur fluctuates widely. Suffice it to say here that when listening to dolphins during zig-zag swimming one hears much vocalization during active sorties, followed by a decline in their occurrence as the animals slow and begin to mill, and that this pattern is repeated over and over.

Table 5. Statistics from multivariate discriminant analysis of spinner dolphin sounds recorded from various behavior states. Behavior periods (labelled groups) were differentiated on the basis of sounds per animal emitted during each period. Four discriminant analyses were run: in the first, each behavior period was considered a single group; in subsequent analyses, behavior periods were lumped.

Discriminant Groups	C1	Function 1	Function 2	P(1)2	P(1)3	V(1)4	V(2)
1 - Descent	Screams	0.002	1.081				
2 - Socialize							
3 - Night	Nonharnomic						
4 - Travel	Whistles	0.688	-0.168	0.01	0.05	91.8%	6.1
5 - Meet							
6 - Rest	Burst Pulse	0.753	-0.781				
7 - Enter							
8 - Spread	Clicks	0.825	0.313				

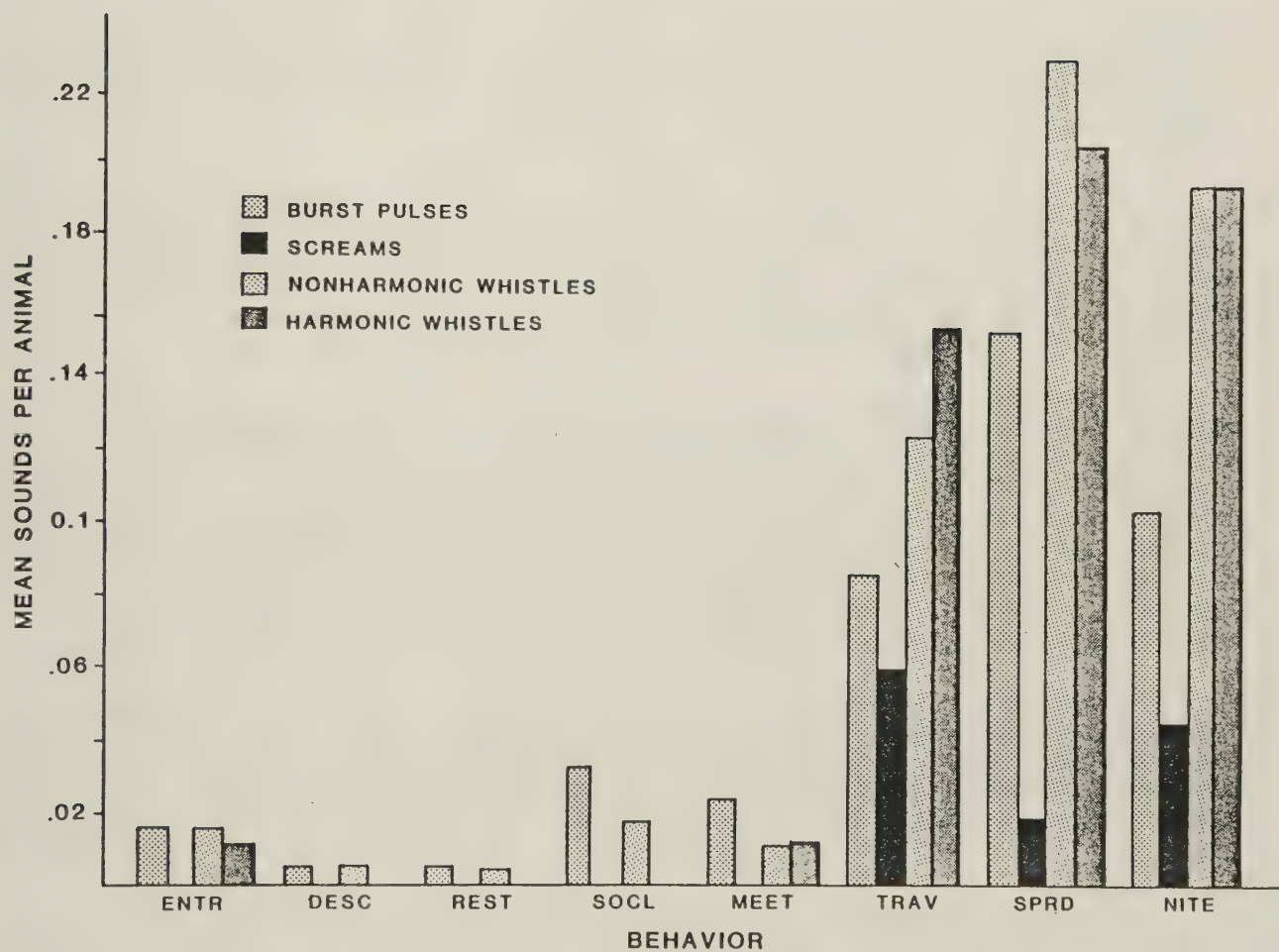


Figure 38. The mean numbers of sounds of various classes, per animal, for different classes of behavior.

Although they emit clicks during all periods, dolphins are nearly silent during rest, and at the opposite extreme may emit up to 7 clicks per animal per five second sampling period during travel and feeding (Figure 39). In our sample of quiet periods, the dolphins emitted no screams, and few whistles or burst-pulse signals. The number of burst-pulse signals rose dramatically as animals began to travel offshore, and continued to increase through the spread formation period (Figures 40-41).

Acoustic samples recorded from schools meeting other schools in the bay were not found to contain distinctive levels or kinds of sounds. The general mix of sound classes and levels of emission were indistinguishable between those recorded from active schools entering the bay, and from schools in which social patterns such as caressing were prominent.

Our results from the study of whistles agree closely with those of Steiner (1980, 1981), who analyzed Atlantic spinner dolphin whistles. He found that such whistles generally sweep upward in frequency, last between 0.02 - 2.4 seconds, and do not have many inflection points. That is, they usually do not sweep up and down sinusoidally in frequency (Table 6).

Spinner dolphin whistles have a contagious aspect. Our tapes of zig-zag swimming, spread, or traveling schools frequently contain clusters of whistles. Periods of up to four seconds without whistles may be followed by times when whistles come in overlapping groups of seven or eight signals. This clustering of whistles was sometimes especially notable in schools at the end of zig-zag swimming as high speed travel out to sea began. Then many school members whistled periodically in interweaving tangles of whistles, followed by quiet periods.

Whistles increased during travel and are very conspicuous during nighttime feeding periods (Figures 42, 43) when they may be 14 times more abundant on the average than during rest. They are even more abundant during spread school periods. Pure tone whistles and whistles with harmonics are given at all times of the day.

Closely similar whistles are usually given in series, presumably from the same animal. Whether or not this represents the "signature whistle" of Caldwell and Caldwell (1965) is presently moot. In our records we have no way to identify individuals beyond assigning a single whistle train tentatively to a single animal. The Caldwells reported that an individual dolphin emits a whistle typical of that individual during much of its life.

Pure tone whistles and whistles with harmonics are given at all times of the day. While they do not vary more than about two fold in frequency of occurrence during the day, such whistles become from five to about ten times as abundant at night (see

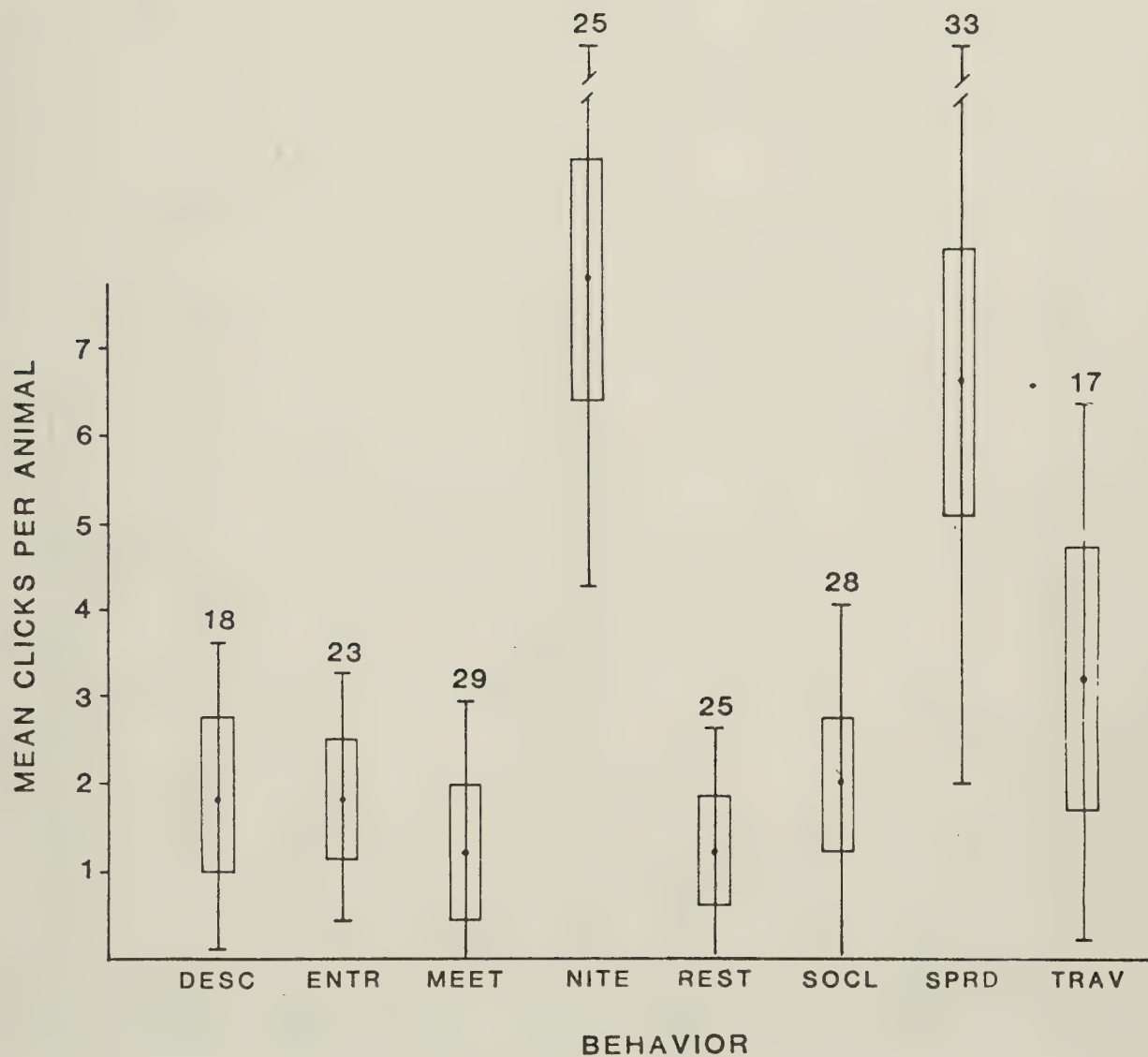


Figure 39. The mean number of clicks per animal per five second period, for different classes of behavior. Bars represent standard deviations, and boxes 95% confidence intervals.

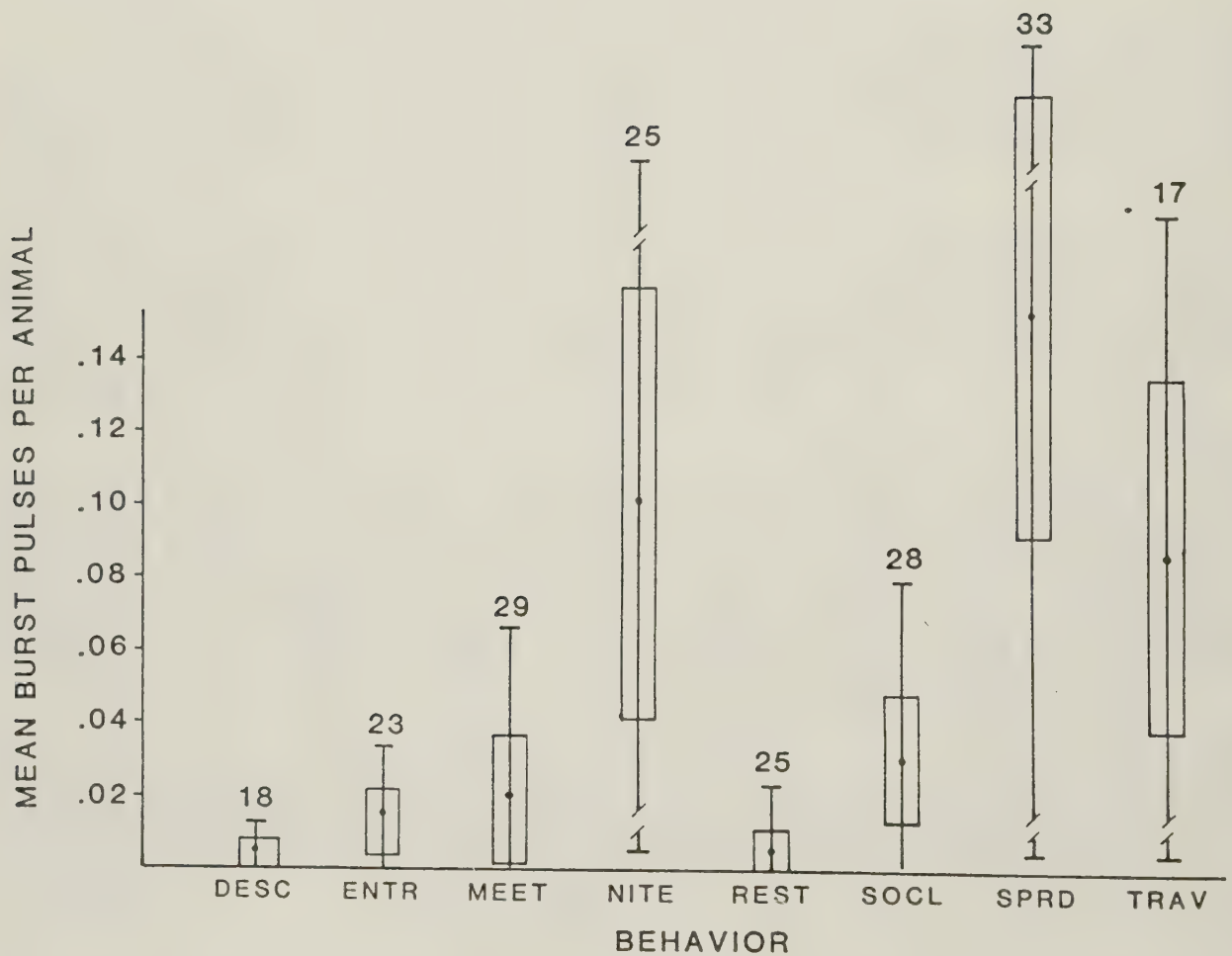


Figure 40. The mean number of burst-pulse signals per animal per five second period, for different classes of behavior. Bars represent standard deviations, and boxes 95% confidence intervals.

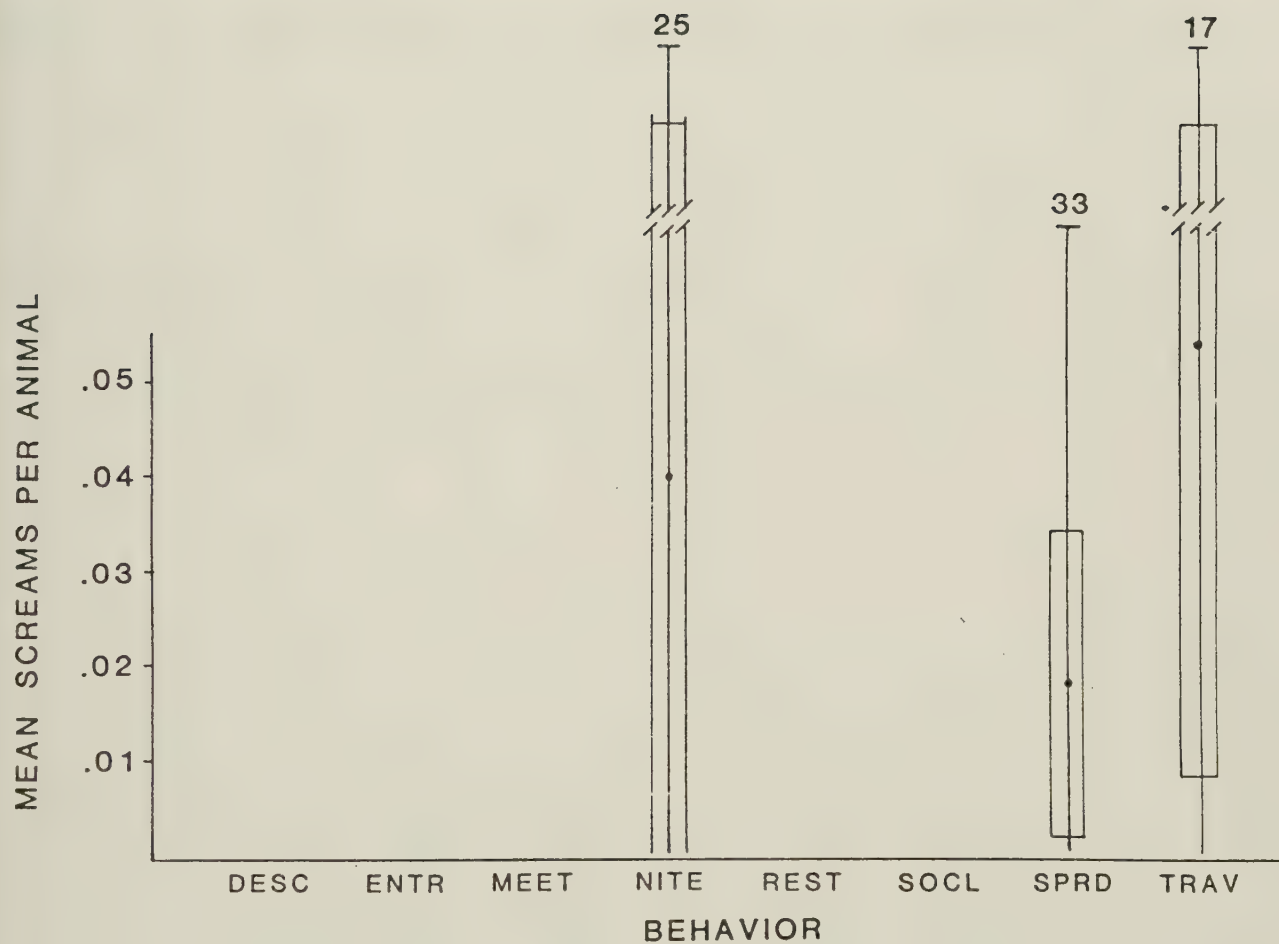


Figure 41. The mean number of screams per animal per five second period, for different classes of behavior. Bars represent standard deviations, and boxes 95% confidence intervals.

Table 6. Statistics for spinner dolphin whistles. Breaks refer to all shifts in frequency, or short stops in emission of a whistle. Inflection points refer to changes in direction in contour of whistle. There are no statistics for some periods (e.g. rest) because there were too few whistles in recordings.

BEHAVIOR PERIOD

PARAMETER	ZigZag (11)1	Enter (25)	Meet (23)	Travel (124)	Spread (92)	Night (114)	Cumulative
Begin Freq. (kHz)	12.77 $\pm$ 0.68	12.06 $\pm$ 1.17	10.85 $\pm$ 0.26	11.12 $\pm$ 0.81	8.42 $\pm$ 0.49	10.50 $\pm$ 0.78	10.42
End Freq. (kHz)	12.45 $\pm$ 1.51	17.86 $\pm$ 0.86	15.08 $\pm$ 0.95	14.55 $\pm$ 0.71	16.74 $\pm$ 0.80	16.98 $\pm$ 0.94	15.85
Duration (seconds)	0.45 $\pm$ 0.13	0.72 $\pm$ 0.13	0.81 $\pm$ 0.13	0.64 $\pm$ 0.05	0.79 $\pm$ 0.10	0.65 $\pm$ 0.05	0.68
Number of Breaks	1.09 $\pm$ 0.86	0.84 $\pm$ 0.50	0.17 $\pm$ 0.16	0.22 $\pm$ 0.10	1.39 $\pm$ 0.51	0.26 $\pm$ 0.14	0.57
Number of Inflections	1.55 $\pm$ 0.66	1.80 $\pm$ 0.53	1.78 $\pm$ 0.57	1.61 $\pm$ 0.24	2.42 $\pm$ 0.72	1.18 $\pm$ 0.21	1.69

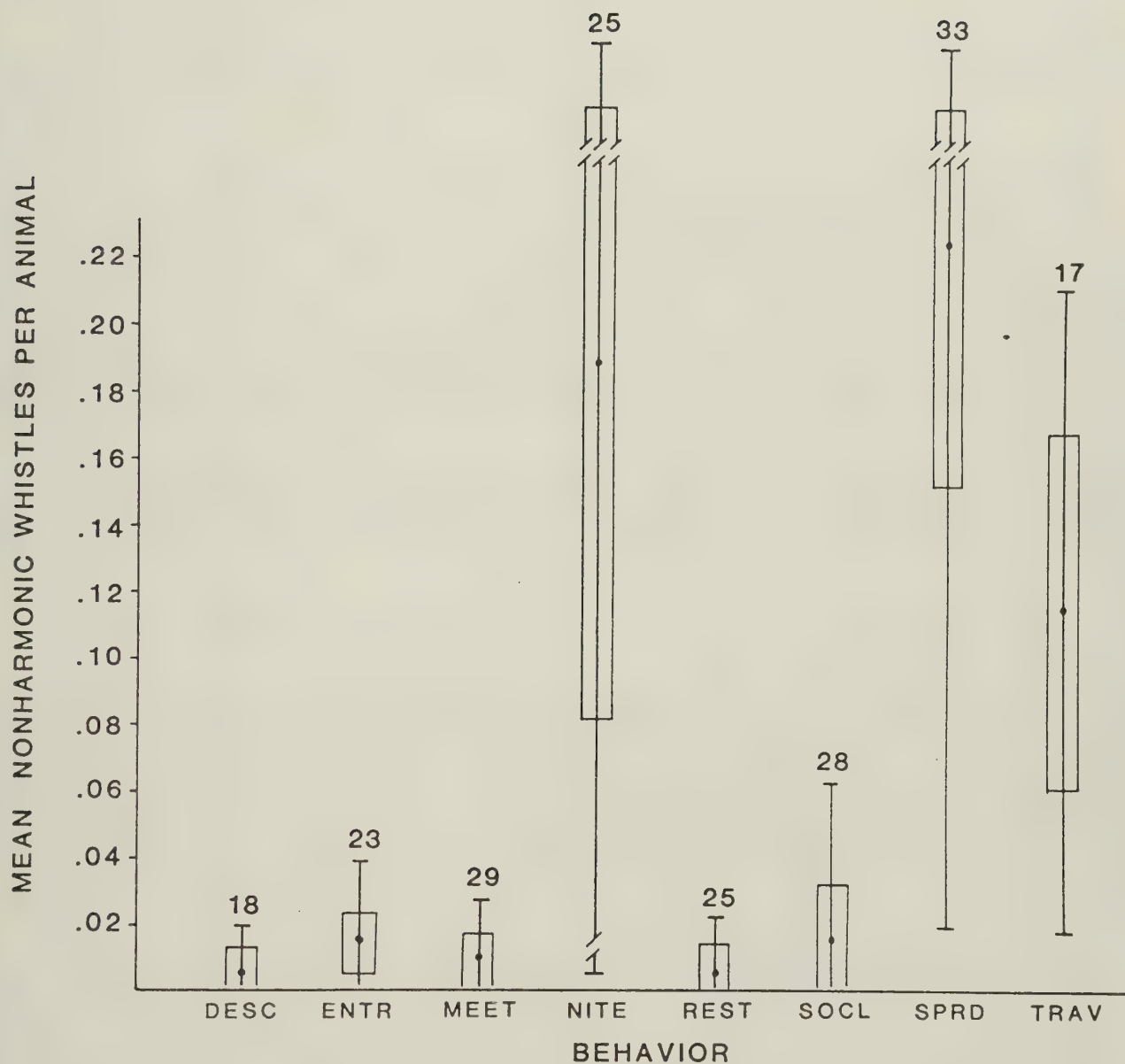


Figure 42. The mean number of nonharmonic whistles per animal per five second period, for different classes of behavior. Bars represent standard deviations, and boxes 95% confidence intervals.

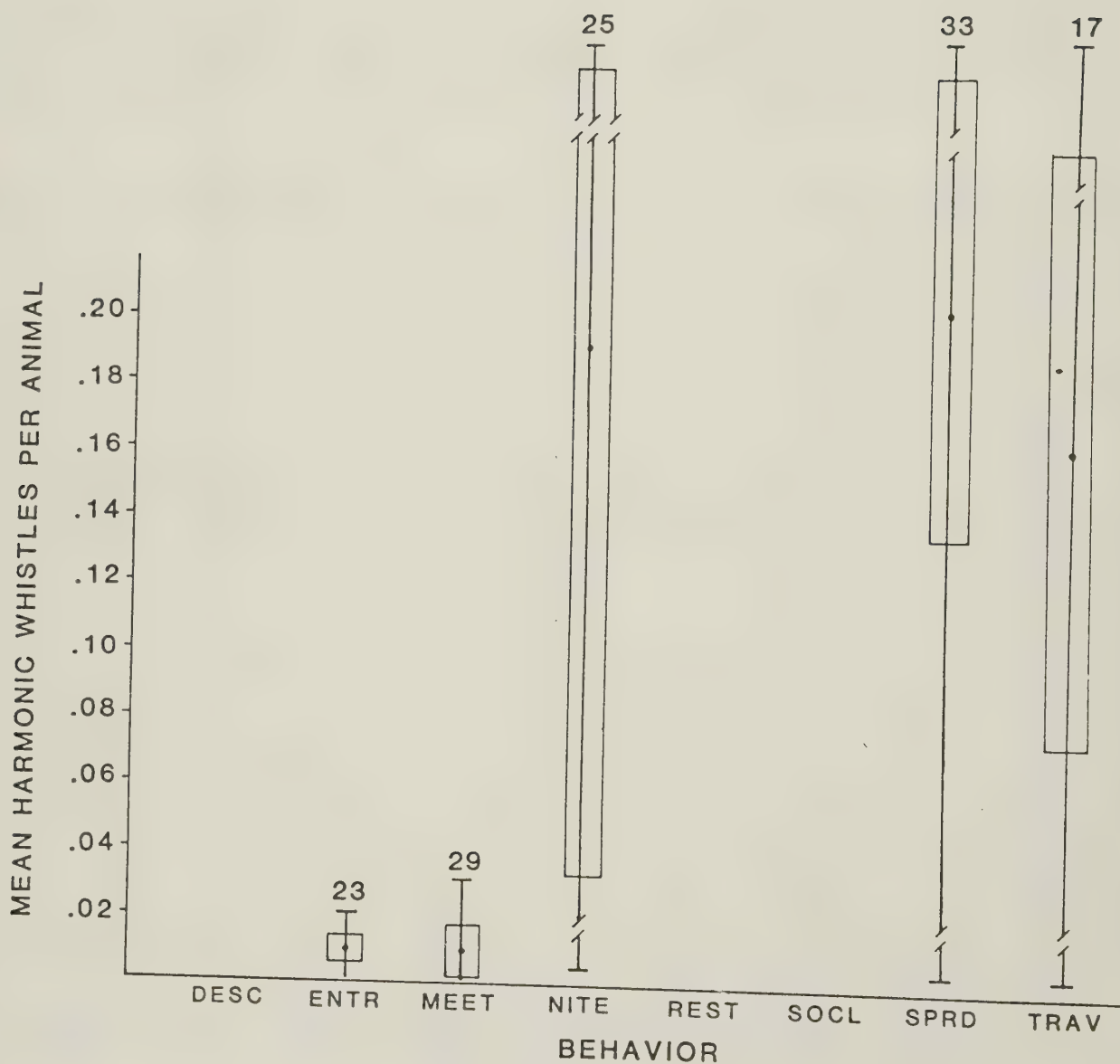


Figure 43. The mean number of harmonic whistles per animal per five second period, for different classes of behavior. Bars represent standard deviation, and boxes 95% confidence intervals.

Figure 42). This interpretation lists entering, descent into rest, socializing and meeting as daytime patterns, and traveling and spread patterns as occurring during dusk.

Screams appear in our data only as schools begin to travel out to sea at dusk, and at night, when they may become quite abundant. No other context is apparent to us at this point (Figure 41).

Click trains are emitted during all classes of behavior, and there is a clear trend in the frequency of their occurrence. They are at a low level during all daytime patterns, being least frequent during rest, and somewhat more abundant during descent into rest and awakening. They become more than twice as abundant during travel out to sea as during rest, which generally occurs near dusk. Once the school reaches deep water and abruptly spreads they typically double again in frequency of occurrence. And, finally, during nighttime feeding they are even more abundant, on the average.

This pattern of changing click train abundance fits the need for acoustic navigation in dark water, but the reader should bear in mind that if clicks also have a communicative function it also fits that model.

3. Interpretations

It is certainly difficult for the scientist, listening to schools of moving animals that are usually out of sight below the water surface, to say what the recorded signals might have meant to the dolphins. But, it is valuable to make such an attempt. Others may then test their observations against such a framework, and the conception can be bolstered or discarded. Several threads lead us toward an interpretive framework that proposes uses for the various classes of dolphin sounds. First, let us consider how whistles might be used.

We propose that whistles are individual identifiers that may be modulated to carry additional analogic information about emotional state, level of alertness, the presence of food or danger, and similar information. We propose that they function as what Jakobson (1960) called a "phatic system of communication." Such a system envisions whistles as providing an open communication channel, and their modulation carries a variety of context-specific information.

The data that lead us to this proposition come from several sources. First, captive studies have established that for the few species observed thus far dolphins emit whistles typical of an individual (signature whistle), and that modulations of it, indicative of various emotionally based states, are superimposed on the basic signal (Caldwell, Caldwell and Miller 1970).

Second, while our animals whistled in all behavior periods, whistle abundance was much greater when animals could not see each other than at other times. Third, there is a clear contagious aspect to whistle emission. The animals are reacting to each other's whistles. Such contagion is greatest when dolphins become aroused from rest.

Finally, unlike click emissions of various sorts, whistles seem to be fairly omnidirectional in nature, and to travel well in the ocean. They sometimes can be heard when click trains cannot. Therefore, they seem to be the class of dolphin sounds best suited to such an open communication channel, available to all schoolmates.

It is useful to examine Jakobson's (1960) communication model further. He described four modes of signaling; referential signals, which refer to specific objects in the environment, emotive signals, which indicate the emotional state of the signaler, vocative signals, which are threats or aggressive signals directed at the receiver, and phatic signals, which provide an open communication channel.

In this scheme we suggest that whistles form the basic phatic system, and that at least referential and emotive information is carried on it by modulations. We further suggest that this system is what allows dolphins to organize their schools at times when they cannot see each other and therefore cannot see visual signals; for example in spread formation, or in the dark.

If this model is correct, the repetitive dolphin whistling we record is doing several things simultaneously. To give an example, in a spinner dolphin school at night an unmodulated signature whistle carries the meaning: "This particular dolphin is here, and all is well". The place, the individual identity and the emotional state of the animal can be carried by a single signal.

The fluctuating occurrence of contagious whistles in zig-zag swimming we interpret as social facilitation, with the dolphins testing each other's alertness until the school is ready for its transit to sea.

From the aggregate of such signals from all school members the disposition and state of the entire school can be carried to all members. The sensory integration function of the school (see Norris and Dohl 1980) can then be carried out in the dark by sound, just as it seems to be performed primarily by vision in daytime rest.

The Caldwell's (1965) found that 99.4% of emitted whistles from captive dolphins were "signature whistles", repeated over and over, ad nauseum. The constancy proved so great that the Caldwell's first erected a kind of one-dolphin one-whistle

hypothesis, feeling that dolphins were possibly incapable of any other whistle production. But these workers later discovered that dolphins have much capability at modifying the basic signal (Caldwell, Caldwell and Miller 1970). Other work with mimicry of sounds produced by machine (Richards, Wolz and Herman 1984) showed that dolphins have extremely refined capability at modifying whistle emissions.

Modulation of the basic whistle to carry emotional information is known. For example, in fear or pain dolphin whistles show sharp breaks or steps in frequency, much like the human voice cracking in times of stress. Such sounds have been recorded from harpooned dolphins (Busnel and Dziedzic 1968). Or, during birth, an animal that normally emitted a whistle composed of a single rising and falling tone (or loop) may link loops together into a continuous series of several loops (Dreher 1966). Such multilooped whistles tend to attract schoolmates, and to cause excitement amongst these schoolmates.

It is worth emphasizing that the basic phatic channel, namely whistles, remains constant when there is no emotional information to convey, as the Caldwells found in captives. There must be a level of invariance in the basic signal or the information about the individual identity, place, and state of a given dolphin cannot be carried by the system. It is not surprising that in captivity, where changes in emotional state may be uncommon, the basic phatic channel is repeated over and over without modulation.

Another relation of whistles has, as we describe earlier, to do with allowing school members to assess each other's alertness. It is probably crucial that all dolphins in a school are alert before they venture into feeding patterns at sea, following a rest period. And in the group processes that govern dolphin school "decision making" testing and consensus seem to be the means by which this is achieved. Such social facilitation is what we suspect is happening when whistle choruses sweep through a school at the end of zig-zag swimming as a school begins its dash out into the darkening sea.

The oscillatory levels of sound emitted during zig-zag swimming, which typically ends as the animals begin their rapid dash out to sea with the interweaving whistle choruses previously described, may therefore represent alertness testing. An animal tests its neighbor's ability to respond precisely in time with an appropriate whistle, and if all are alert a chorus ensues. If all are not alert, the school subsides both in locomotion and vocalization for a time and the testing begins anew. The phonation thus becomes oscillatory, just as we have observed it to be.

There are many parallels for these interpretations from studies of other mammal herds and from studies of flocking birds. The movements of jackdaw flocks seeking roosts in the evening is

cyclical, and changes in direction occur in a manner strikingly reminiscent of spinner dolphins during zig-zag swimming (Lorenz 1952). Similarly reminiscent is the "pseudopod movement" of hamadryas baboons (Papio hamadryas) (Kummer 1968). Piñon jay flocks circle and call before determining migratory direction (K. Norris, pers. obs.) and the development of behavioral synchrony and preparedness of gelada baboons is communicated through chorusing (Richman 1980).

Perhaps the most striking parallel is found in the "pep rallies" of Cape African hunting dogs (Lycaon pictus). Estes and Goddard (1967) describe the twittering calls of these dogs made prior to going on the hunt. As each animal wakes it joins its pack mates in a chorus of twittering and touching muzzles (note that caressing is also prominent during the active phases of spinner dolphin zig-zag swimming) prior to going on the hunt. The intensity rises and falls as the dogs start out as if to move off, and then come back to their sleeping grounds. Finally, the entire pack moves off in unison.

During the hunt, the dogs use calls, apparently to locate each other spatially. Estes and Goddard suggest that the so-called pep rallies serve to inform individuals of the readiness of the pack to hunt, to excite and alert the pack, and to reaffirm relationships between pack members. All of these features seem to occur with spinner dolphin schools during zig-zag swimming. In the fluid spinner dolphin society such choruses may also reacquaint individuals with the whistles of others they should expect to hear that evening.

Next, a few comments on burst-pulse signals are in order. In primates, canids, and dolphins, burst-pulse signals probably have similar contexts; spectrally rich growls, purrs, buzzes, barks, mews, etc., are used as emotive and vocative signals between individuals (Fentress 1967, Marler 1968, Green 1975, McCarley 1975, Lehner 1978, Petter and Charles-Dominique 1979).

Spinner dolphin burst-pulse signals range from almost private "chuckles" that pass between courting adults, to preemptory barks or loud "bangs" used as aggressive signals. Such sounds sometimes travel long distances. We have listened to burst-pulse signals issuing from a school traveling against the cliff of Kealake'akua Bay, from a craft drifting at the entrance to the bay, more than 1.6 km away from the dolphins.

If burst-pulse are emotive and vocative signals we would expect to see the greatest number of them during socializing periods, when animals are in close physical contact, rubbing bellies, chasing one another and exhibiting 'sexual' behavior. We might also expect a high incidence of burst-pulse signals when two schools meet. Other animals exhibit a wide range of such sounds when greeting each other. Chimpanzees, for example, use a number of such acoustic signals indicating recognition and degree

of friendliness, when they meet (Marler 1968, Marler and Hobbett 1975).

Our statistical data do not support this conclusion cleanly. The number of burst-pulse signals during daytime socializing periods and the meeting of two schools is intermediate between low activity periods (entering the bay, descent into rest, and rest) and periods of travel, spread formation and nighttime feeding, when burst-pulse signals are very common.

Nonetheless, data from other delphinids support the proposition that burst-pulse signals are emotive and vocative in nature. Tyack (1976) found that bottlenose dolphins emitted the greatest number of burst-pulse signals during milling periods when the animals also exhibited sexual and play behavior.

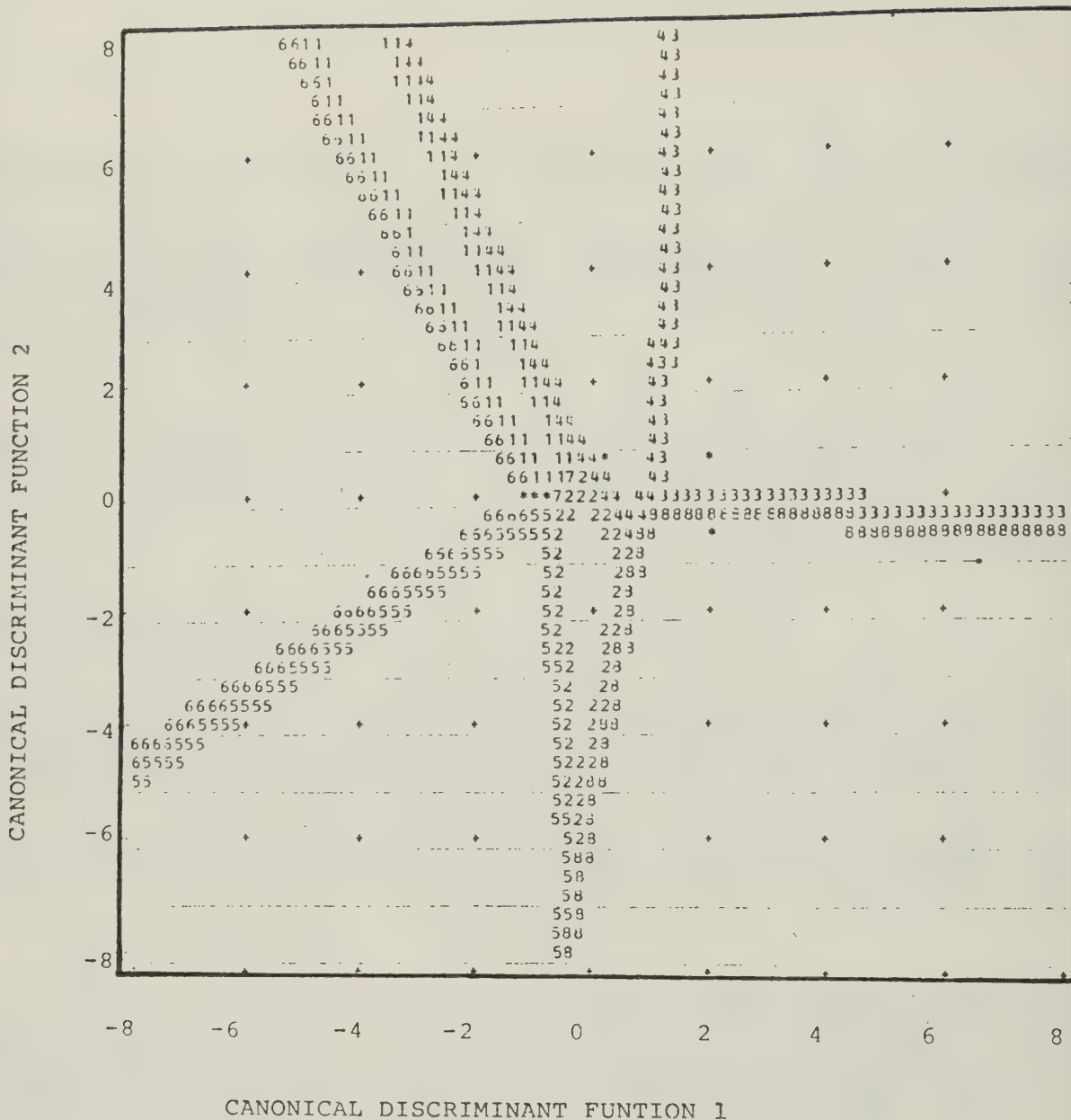
Our conclusion is that all daytime acoustic patterns are probably to some degree depressed as compared to sounds emitted at dusk or in the dark (Figure 44). Traveling and feeding schools seen at dusk were certainly the sites of very active social behavior, in which chases and caressing behavior seemed to be even more frequent than during daytime socializing periods. It is probable that both vision and sound emission are important during these times, while only sound is effective at night.

The only period when spinners apparently cease highly interactive patterns is during rest, and this is a time when they emit virtually no burst-pulse signals.

Individual Identification

During the 18 months of the study, from May 1979 through October 1980, and during two weeks in June 1981, 224 individual dolphins were identified from photographs (Figure 45). Thirty two of these identified animals were determined by body marks which are infrequently resighted. The remaining 192 dolphins represent the main body of our identification work. Sixty-six of these were sighted only once. Of the 126 dolphins sighted more than once certain animals were seen repeatedly.

Thirty-six dolphins were sighted 10 or more times each. These most easily recognized individuals provided the majority of data on long term associations and movement patterns. However, many of the animals that were sighted less often were readily identifiable from clear photographs; they simply appeared less often in our study area. Herein lies a dilemma; we cannot determine why a particular animal was infrequently present in our photo log. It could have been missed because of the subtlety of recognition marks, because it tended to stay out of the range of observers and their cameras, or it could have been missed because it was seldom present. And, finally some bias doubtless exists



- | | |
|-------------|----------|
| 1-Descent* | 5-Meet |
| 2-Socialize | 6-Rest |
| 3-Night | 7-Enter |
| 4-Travel | 8-Spread |

*Behavior Periods

Figure 44. Two dimensional plot of multivariate discriminant functions for various classes of sounds, by behavior period. The diagram indicates which behavior periods are closest to each other in terms of sounds emitted. For example the daytime nearshore behavior classes; Rest (6), Descent (1), Meet (5) and Socialize (2) are difficult to discriminate by sound while they are easily separable from nighttime functions. See Table 5.

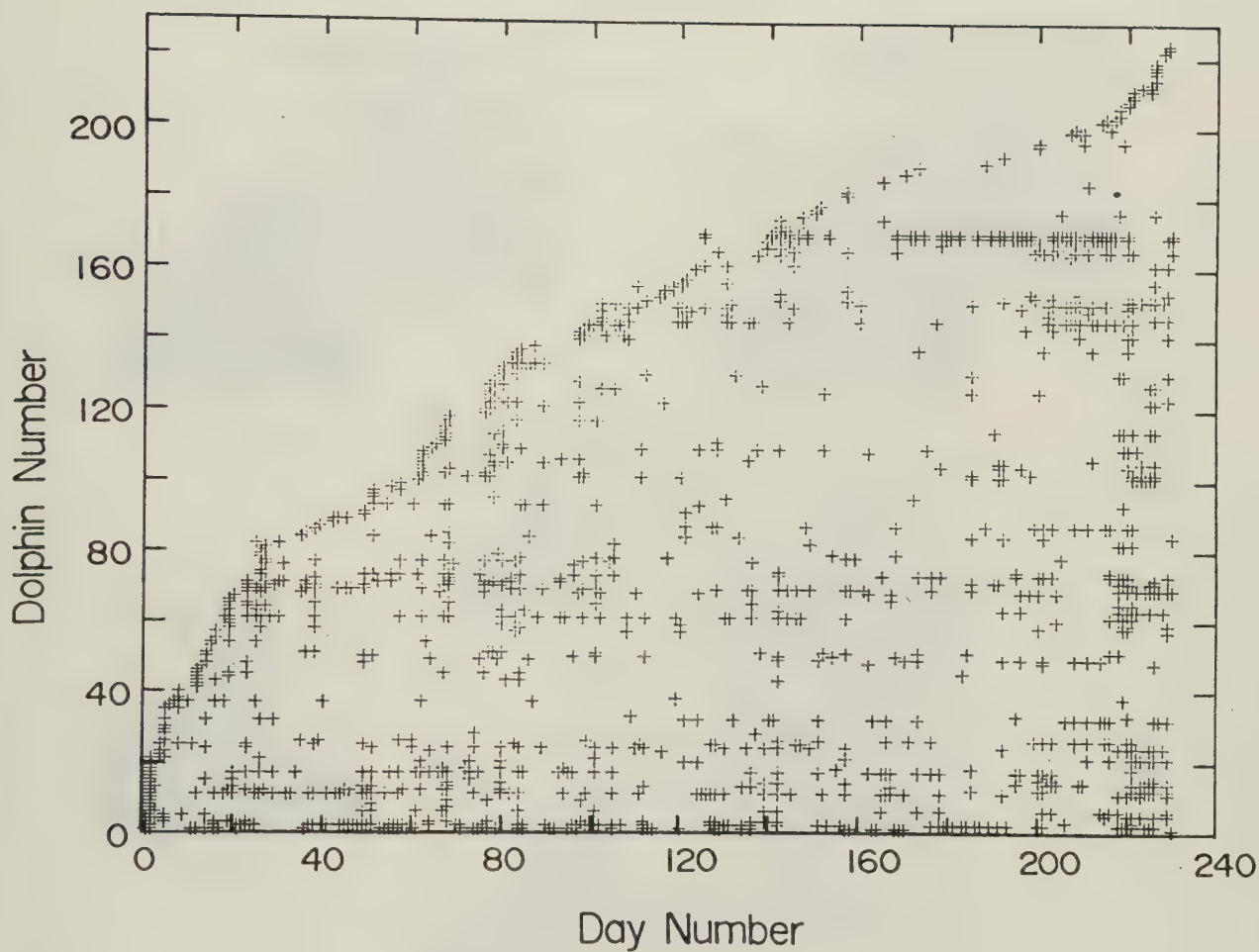


Figure 45. Cumulative record of sightings of marked dolphins during 230 sighting days, along the Kona Coast of the Island of Hawaii, May 1979 - October 1980, and June 1981.

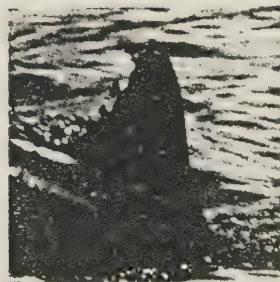


5 June '79

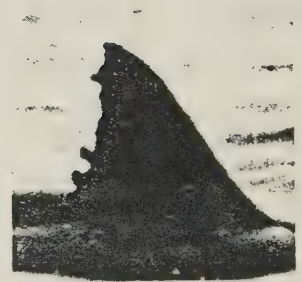


17 May '80

Dolphin #1

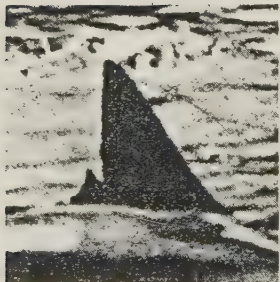


11 April '80



11 June '81

Dolphin #2



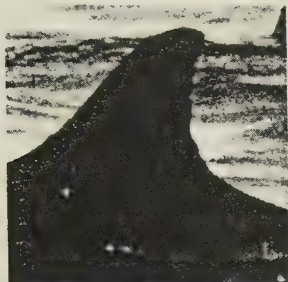
4 August '79



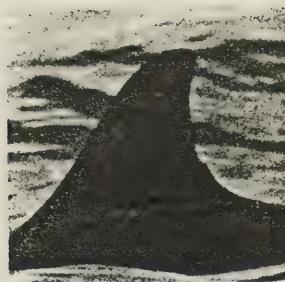
21 September '80

Dolphin #17

Figure 46. Some well-marked and frequently sighted dolphins. Photographs were taken in different years and show changes in marks. Dolphins #2 and #17 underwent dorsal fin changes during the study, but remained clearly recognizable. Dolphins #27 and #31 were almost always seen together.

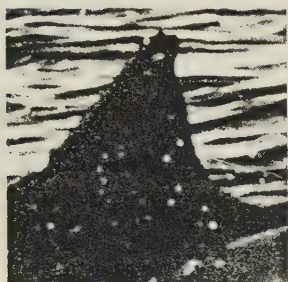


5 June '79



9 June '81

Dolphin #15

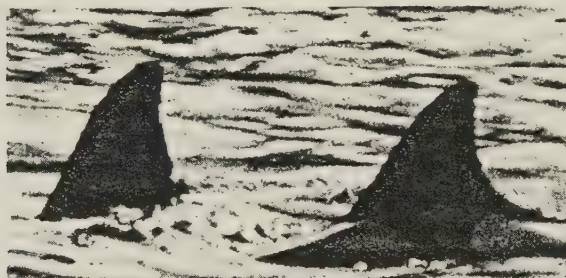


25 October '79



11 June '81

Dolphin #101



22 May '79



5 June '81

Dolphins #27 and #31

against seeing animals whose marks changed throughout the study. Judging from the constancy of most marks this was probably a minor factor.

To obtain information on differential use of areas along the Kona coast of the Big Island we divided our study area into four major sectors: (1) Kealake'akua Bay, (2) south of Kealake'akua Bay to and including Kauhako Bay, (3) north of Kealake'akua Bay to and including Kailua Bay, and (4) Keahuolu Point to Kukio Bay in the northernmost section of the lee coast. The occurrence of recognizable dolphins in these four areas is shown in Figures 47-50. This record does not include data from Makalawena area north of Keahole Point.

There was a total of 1233 recognizable dolphins sighted, with 795 in Area #1, 119 in Area #2, 134 in Area #3, and 185 in Area #4. The different number of sightings for each area does not reflect differential use of these areas by marked dolphins, but predominantly the amount of effort we put into surveying the four areas.

The average number of sightings per animal was 6.4, ranging from 1 to 69 sightings.

A computer program (written for the Hewlett-Packard 9825 computer) calculated frequency of sightings per number of total sightings per area per dolphin. The results allowed us to compare relative frequencies of occurrence by area, standardized for sighting effort. The 36 dolphins seen 10 or more times demonstrate that indeed different groups of dolphins spent more time in some areas than in others. Ten of these dolphins were mainly seen in Kealake'akua Bay, and to the north of it. Six were seen throughout the south, but not north of Kailua Bay, and another six were seen only north of Kailua Bay. Eight individuals were seen mainly south of Kealake'akua Bay, and seldom in the bay or to the north of it. Only six of the 36 dolphins were seen with about equal frequency throughout the study area. Time analysis showed us that this overall frequency of occurrence was due to shifts from one area to another. Thus, dolphins #11, #12 and #14 were first seen in Kealake'akua Bay, but they shifted to the Keahole Point area to the north, when not present in Kealake'akua Bay.

On a more refined level, we have analyzed association patterns between animals. Dolphin #1 (Finger Dorsal) and #2 (Four Nip) were seen together on 26% of their total sightings (#1 was sighted 44 times and #2 was sighted 69 times), throughout the year and throughout the study area. But the association appeared to be quite fluid. This is exemplified by a series of sightings in Kealake'akua Bay in September 1979, in which #1 was observed in the Bay on September 4 and 5, both were observed in the Bay on September 8 and 11, and #2 was observed on September 15th. Although there is a slight possibility that these dolphins were

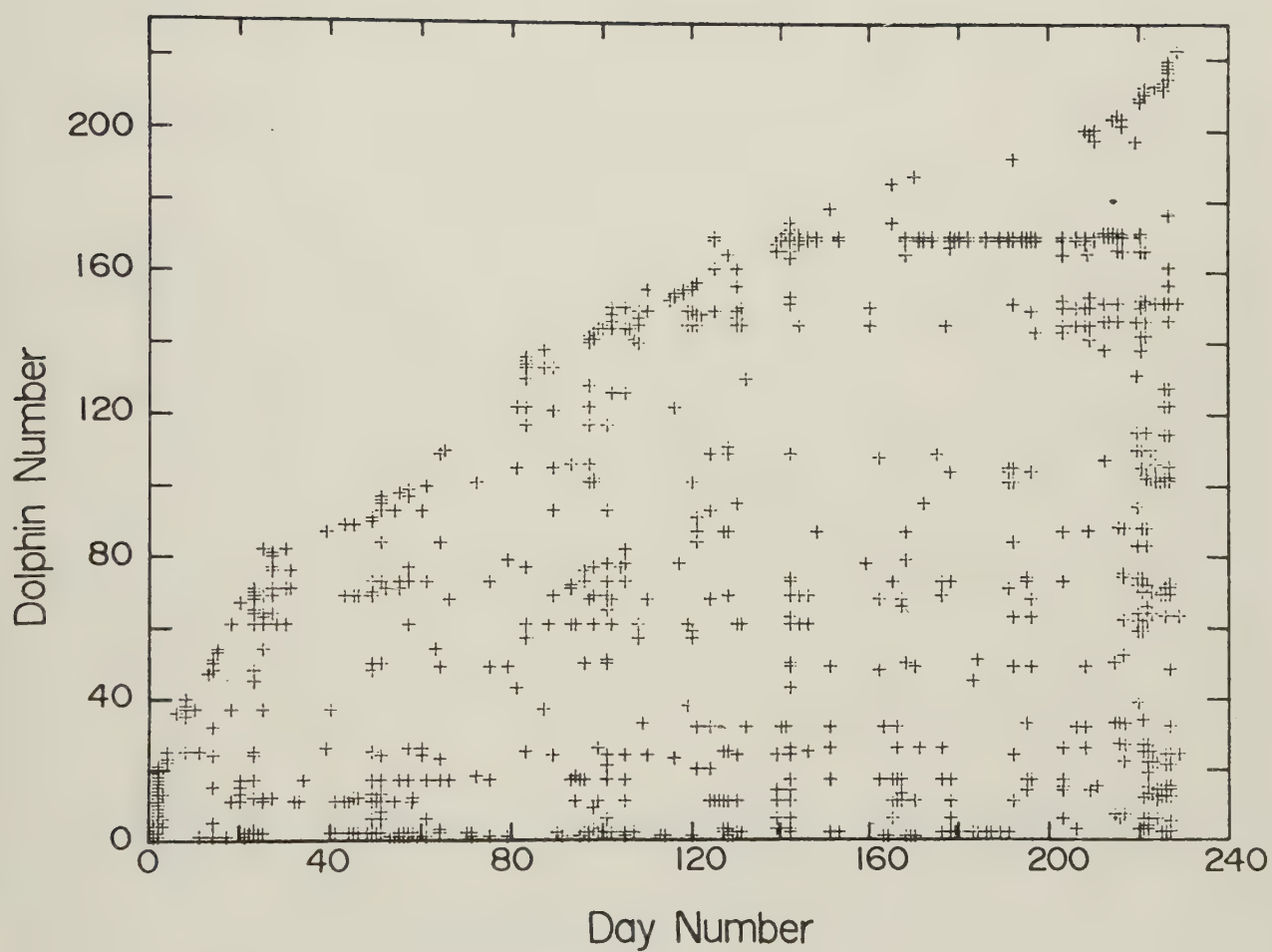
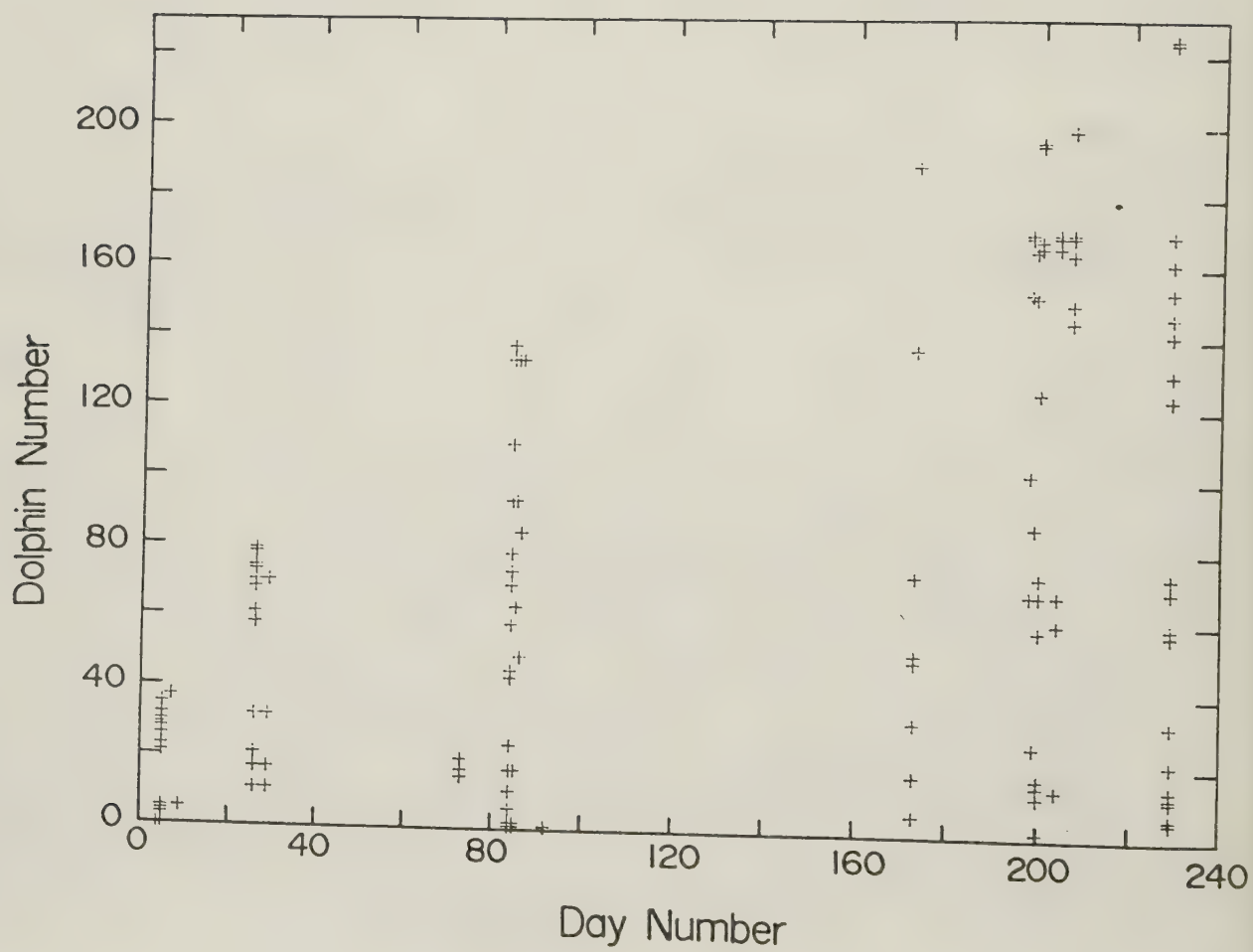
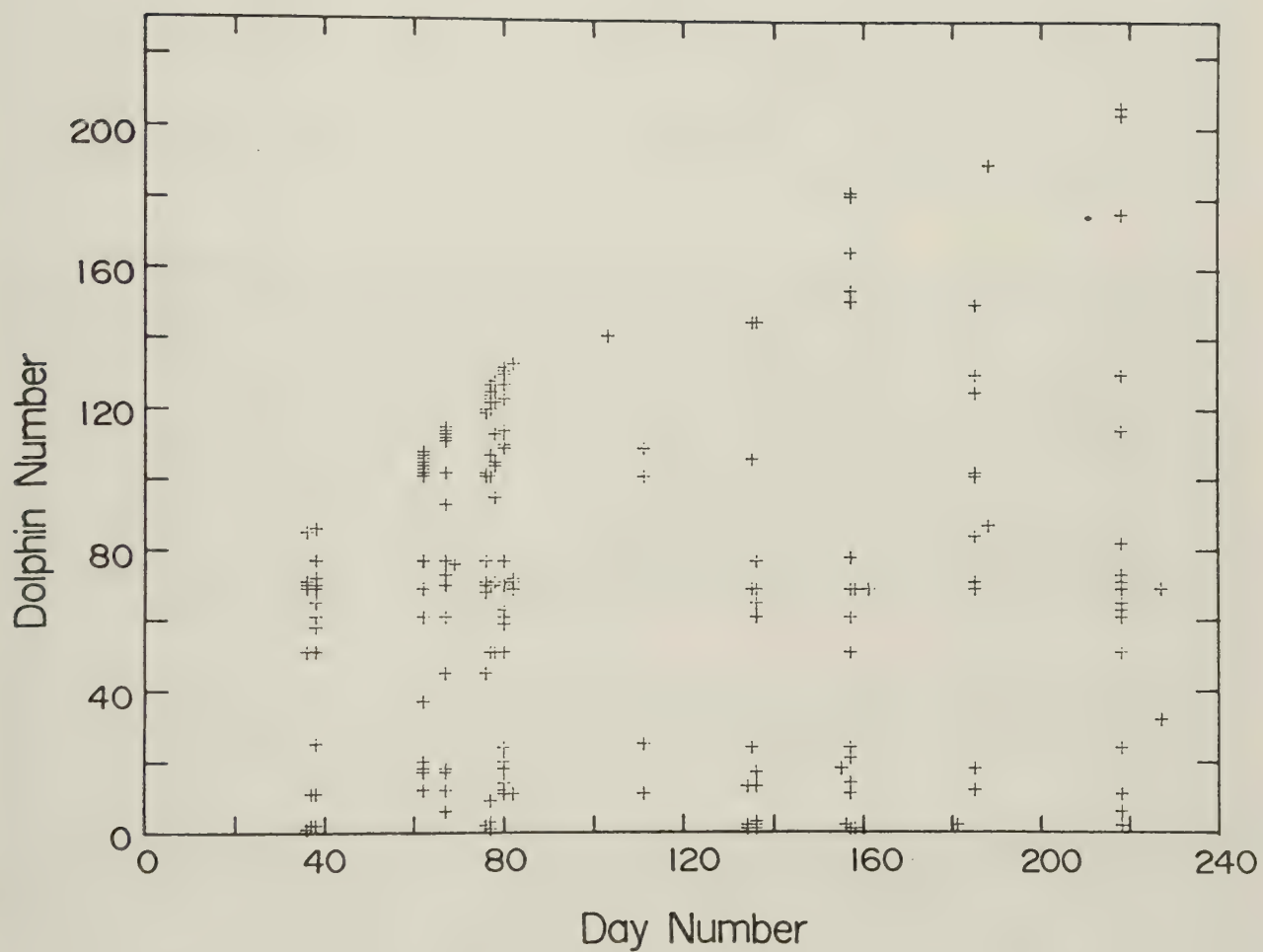


Figure 47. Cumulative record of sightings of marked dolphins during 230 sighting days within Kealake'akua Bay.





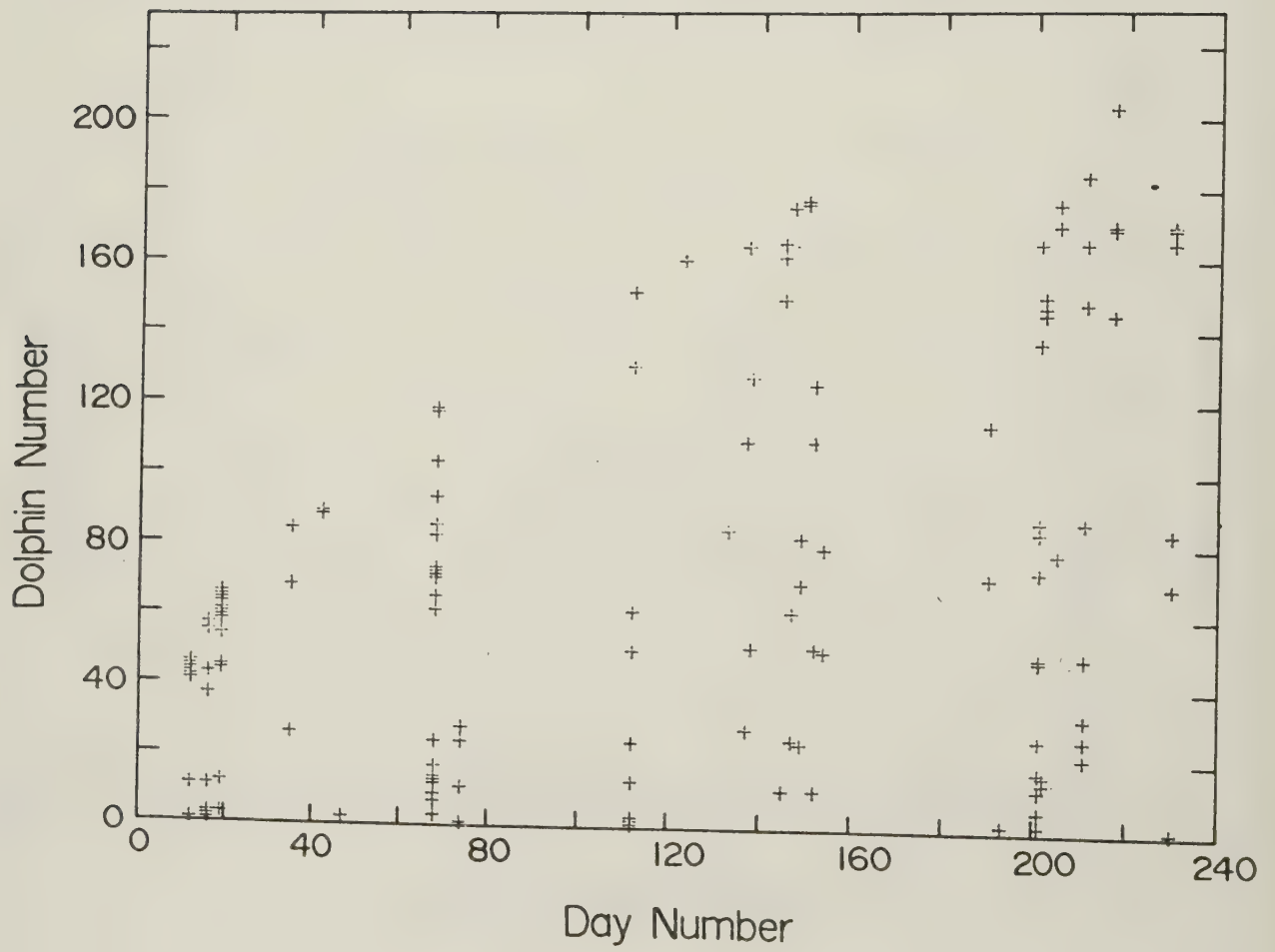


Figure 50. Cumulative record of sightings of marked dolphins north of Kailua Bay.

together on days when only one was noted, both dolphins are highly distinctive, can be determined from both sides, and it is not likely that on good photographic days, such as these days were, one or the other was missed.

Dolphin #1 (Finger Dorsal, a very distinctive animal) was sighted first in Kealake'akua Bay on May 1, 1970 (Thomas P. Dohl, personal communication). During our study the animal was seen in Kealake'akua Bay through July 1980, but disappeared and was not seen again until it was photographed by Shannon Brownlee in December, 1980. Then in a brief study in June 1981, the animal was again missing. It is instructive to follow this often sighted animal in more detail. As Figure 51 shows #1 was quite often seen outside Kealake'akua Bay during May 1980. At this time it was most often seen at Makalawena in the northern sector of the Kona coast. Then it disappeared altogether from our study area.

Dolphins #17 and #73 almost always occurred together. They were both present on the Kona coast except during February and March 1980. Dolphins #165, #87, #152, and #26 comprised a distinct group that seemed to develop during our work. After September 16, 1980 they were always seen together in larger schools, while before this time they were only sporadically. Dolphin #142 (Twin Peaks, a very distinctive animal) was seen five times off Makalawena in the north, from November 1979 to April 1980, and once (December 1979) in Kealake'akua Bay. It was seen on the Kona Coast at no other time even though it was easily distinguishable from a considerable distance. On June 16, 1981, we sighted this animal on the opposite side of the island near Hilo Bay, about 180 km from Makalawena.

It is apparent, as Norris and Dohl (1980) outlined, that spinner dolphins have highly labile school structure but that some associations of individuals and attachments to certain areas also exist, at least temporarily.

It is apparent from Figure 45 that newly-recognized dolphins appeared in our log at a rather high rate throughout the study. During approximately the first 30 sightings the high recruitment rate of new animals must have been due mostly to the newness of our effort. We were cataloguing an unknown population. After about 30 days the number of new animals decreases slightly, but the curve did not level off during the entire study. This indicates that the total "population" of the animals must be large and that its boundaries lie beyond our study area. Since some recognized animals disappeared during our work, and since the general number of animals we sighted in the study area remained relatively stable, we come to the conclusion that efflux must roughly equal influx.

Some animals seem to "visit" the study area from time to time while others seem like strangers that are "just passing through." In other words there appears to be a core area for any

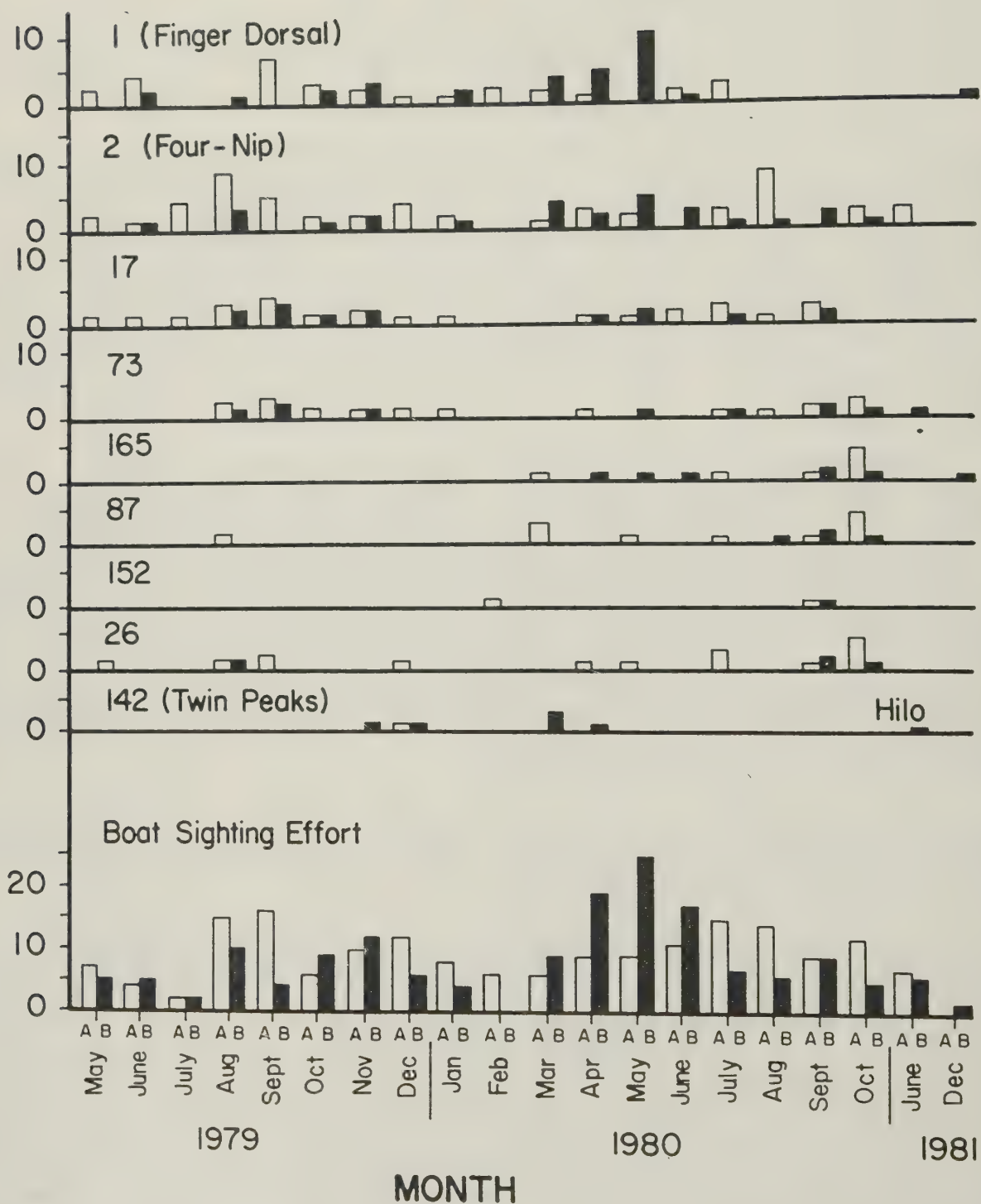


Figure 51. Sightings per month of nine selected dolphins in Kealake'akua Bay (unshaded) and outside bay (shaded). Sighting effort per month is shown at bottom of figure.

particular individual, with a decreasing probability of finding that dolphin farther from its core area. Such hypothesized core areas certainly overlap extensively. This concept was displayed most dramatically by dolphin #142 (Twin Peaks) which was seen briefly on the Kona coast, especially in the north, and then on a single sampling day, on the other side of the island near Hilo. It is tempting to speculate that #142 was a "Hilo animal" but more sightings are needed to draw this conclusion.

1. Interpretation

A model that includes the various pieces of data we have derived is that the Island of Hawaii has an approximate carrying capacity of dolphins, perhaps defined by the size and occurrence of rest areas (each of these seems to hold a fairly specific maximum of animals) and that it draws the dolphins from a larger population. This reservoir may be found in those animals that swim along the island coast but do not enter bays during the day, it may come from farther offshore, or it may come from the island areas of Lanai-Molokai-Maui to the north, or both.

The question of whether we deal here with familial units or larger, learned associations beyond effective familial boundaries is an important one. Suffice it to say that the thousand or so animals that must be involved in this population exchange is considerably beyond effective (from the genetic standpoint) familial units, regardless of their source. But we cannot say whether or not kin relationships are or are not maintained within this larger population.

Abundance

We prepared a sample of 20 good sighting days during which we believed our photographic record to be complete for schools we photographed and all recognizable animals noted. When we compared these data with our group size estimates, on the average 20% of a group was recognizable (14-36%). Since by the end of the study (by scars and marks visible in air) we had recognized 192 animals, we may estimate a minimum number of animals within the population that involves the Kona coast. This is 960 animals (192×5). Of course not all these dolphins are likely to be on the Kona coast at any one time, or at least within the inshore population we sampled. Instead they appear to be spaced around the Island of Hawaii, or offshore, as is suggested by aerial flights, or around adjacent islands.

The numbers of dolphins sighted per aerial survey varied greatly during the study (Figure 52). The minimum estimates of dolphins-per-flight ranged from 59 to 475; the maximum estimates from 75-515. These numbers were based upon best estimates from aerial sightings, and when possible upon counts from photographs taken from the air. Counts provided by experienced observers

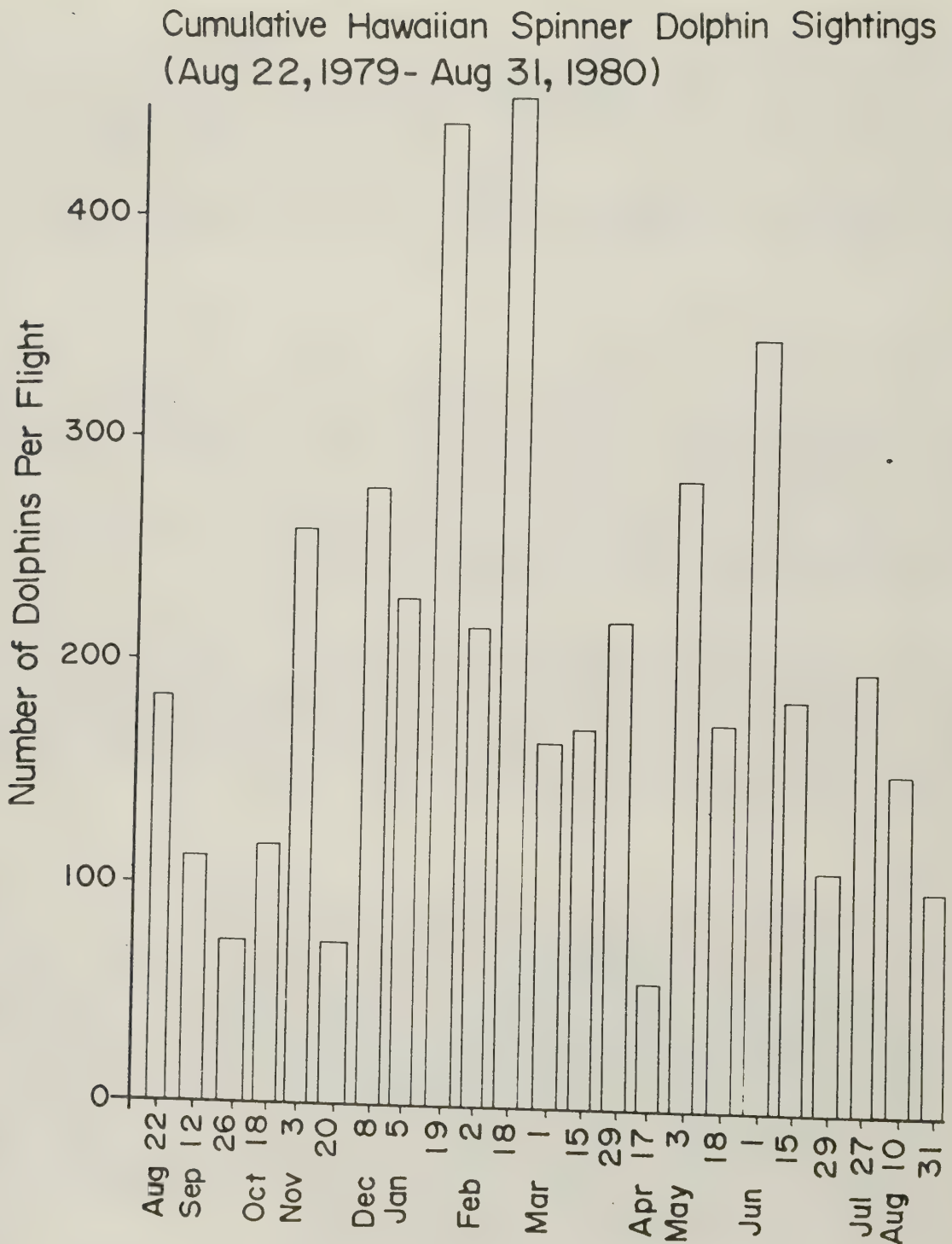


Figure 52. Cumulative spinner dolphin sightings from aerial surveys. Bars represent the sum of minimum estimates or counts from photographs for all sightings during each flight.

were used preferentially when a major disparity existed.

Though there is much variability in numbers of animals sighted between flights, viewed in terms of annual patterns our short data set is inadequate to define population shifts precisely. Grossly, winter numbers tended to be high (November-February) and summer numbers low (July-October). But individual flights sometimes reversed this pattern (November 20, 1979). All such variation could have been relatively constant. Nonetheless the periods August-October, 1979, and August 1980, were especially different with fewer dolphins (100-140) sighted per flight, than the average.

There exist a number of possible explanations for the observed variations in numbers of dolphins observed per flight. These include variations in sighting conditions, number of experienced observers aboard the aircraft, changes in dolphin group size or activity levels, surfacing-diving patterns, and immigration and emigration of dolphins from the area.

Sighting conditions, especially sea-state, lighting and atmospheric turbulence, varied greatly around the coast of the Big Island, and varied within coastal sections seasonally. Generally the waters along the north coast, between Mahukona and Laupahoehoe, and the south coast between Kauna Point and Apua Point provided the worst conditions for sighting spinner dolphins. Rough seas, with extensive whitecapping, were the rule in these areas. The section between Mahukona and Kiholo Bay, on the northern Kona coast, and between Laupahoehoe and Apua Point on the northeast coast were generally better for spotting dolphins. The Kona coast between Kiholo Bay and Kauna Point was the most consistently good for sighting animals. Overall, sighting conditions were better during November through July than at other times.

Both the numbers of schools and the numbers of dolphins within schools appeared to be directly related to sighting conditions. The largest numbers of both schools and constituent animals were observed in winter (schools: $r=0.89$, $n=4$, $p<0.05$; total numbers of animals: $r^2=0.93$, $n=4$, $p<0.05$) when sighting conditions were best, and the least during August-October when conditions were worst. Whether there is an actual relation of the numbers of schools and animals to bad weather or to our ability to see is not clear.

While there were generally two or three observers aboard the aircraft in addition to the pilot, the degree of experience of these observers inevitably varied from flight to flight. At least one experienced observer was aboard each flight, and during January and February 1980 an experienced humpback whale observer was also aboard. We might conclude that the increased number of experienced observers was determinative, but we are given pause by the February 2, 1980 flight when relatively few dolphins were

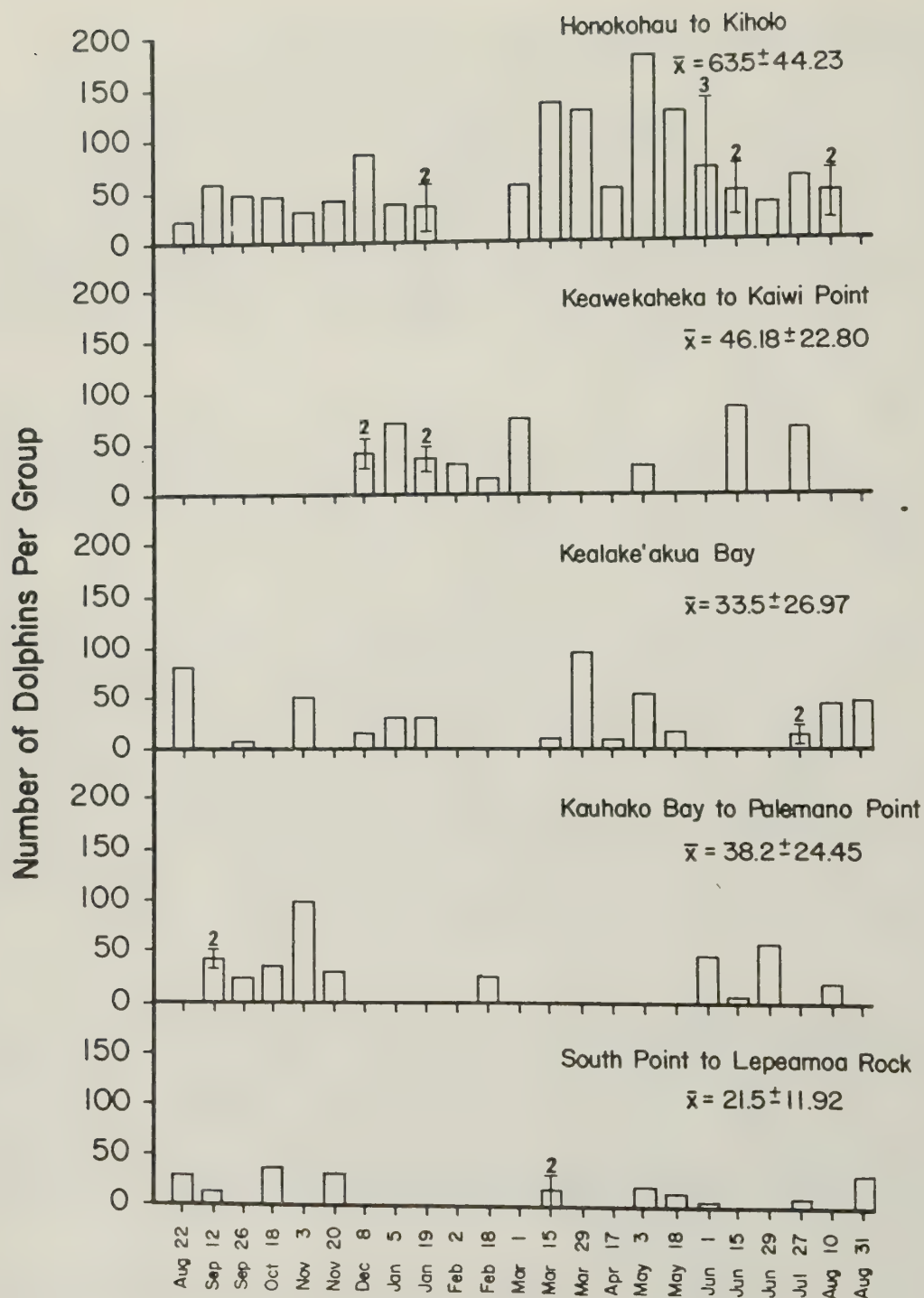


Figure 53. School size estimates from five sections of the Kona coast. Estimates are minimum estimates of observers in aircraft, or counts from photographs. See Figure 2 for place names and locations. Numbers over bars represent numbers of schools in the estimate.

sighted even though conditions were otherwise optimum.

School size may have influenced the probability of sighting spinner dolphins. Schools consisted of from four to approximately 220 individuals. Large schools not only produced much more disturbance at the water's surface than small ones, but also increased the probability that some animals will be at the surface engaged in aerial behavior at any given time. School size varied significantly by area around the coast of the Big Island. The following coastal sections are arranged in order of decreasing mean school size: (1) Upolu Point to Hilo (2) Kiholo Bay to Upolu Point, (3) Honokohau to Kiholo Bay, (4) Keawekaheka Point to Honokohau, (5) Hilo to Cape Kumukahi, (6) Kauhako Bay to Palemano Point, (7) Cape Kumukahi to South Point, (8) Kealake'akua Bay, and (9) South Point to Kauhako Bay. This ranking may involve both seasonal changes in school size and the already demonstrated tendency for given bays to hold only schools of a given size or smaller. This, for example, is probably why Kealake'akua Bay ranks eighth even though it is more regularly occupied than most other parts of the Big Island coast. Seasonal variations in school size seem clearly to occur (See Figure 53).

1. Interpretations

Movement in and out of nearshore waters off the Big Island may account for the variability in abundance estimates. Or, this variation could have been an artifact of sighting difficulty. Potential errors in our sighting data do not allow us to choose among the models that would explain this variation. With a longer record perhaps this choice would be possible. If a movement from an offshore population reservoir exists both seasonal changes in abundance and the sporadic occurrence of marked animals could be explained. Certainly our radiotagging results support such a model.

Most dolphins seem to inhabit particular sections of the coast but occasionally make longer movements, sometimes around the Island of Hawaii.

There may be a seasonal movement around the coast of the Big Island as is suggested by decreases in number of animals sighted on the Kona Coast at the same time that numbers are rising along other coasts (see Distribution). The population seems not to be closed, however, as new animals were added to the "scars and marks catalogue" throughout the study, and at nearly uniform rate once the initial flush of cataloguing was past. The only record we have for Hawaiian spinner dolphins more than a few kilometers at sea is a sighting record by Wayne Perryman of NOAA, who reported schools approximately 45 km off the coast of the Island of Hawaii (personal communication).

A calculated population of spinner dolphins of 960 animals was arrived at from the mark-resighting analysis. Radiotracking data suggested that one reservoir of animals may be close along the shore and be a part of nighttime feeding aggregations.

2. Comparisons of School Size Estimates.

How comparable are schools size estimates taken in various ways? The question is an important one because various extrapolations such as population size may derive from such estimates.

In this work school sizes were estimated from a cliffside theodolite station, by experienced and unexperienced observers in aircraft, from a shore station at just above sea level at our Base Camp, and from shipboard. Some of these were compared to counts made from aerial photographs, and to each other. These comparisons were presented in Figure 54. In general, the aerial observers were in best agreement with aerial photographs when schools were small. As school size increased the tendency for observers to overestimate increased, especially when schools of more than about 120 dolphins were involved. Experienced and inexperienced observers were generally in close agreement when schools were small. Estimates from the theodolite station were usually close to photographic data (eight records). However, it must be remembered that estimates from the theodolite station resulted typically from several hours of continuous observation of a given school. The comparative data for shore and boat stations are too few for analysis.

Association Patterns and Direction in Dolphin Schools

Dolphin schools are clearly reaction systems, just as are fish schools, bird flocks or herds of grazing animals. The interactive patterns between dolphins should then define the shape of the school, or what we term here the "school envelope".

These interactive patterns will be based partly on reactions to stimuli from the world outside the school, and partly the reactions of animals within the school to each other.

This conceptual framework allows us to attempt isolation and definition of the causal factors regulating the deployment of animals within a school.

To give an example, it is widely true that when flocking or schooling animals are frightened their groups tend to tighten (Miller 1922, Major 1976). This happens with all odontocete schools with which we are familiar. The assumed cause is that the tighter the school the more precise or rapid evasive

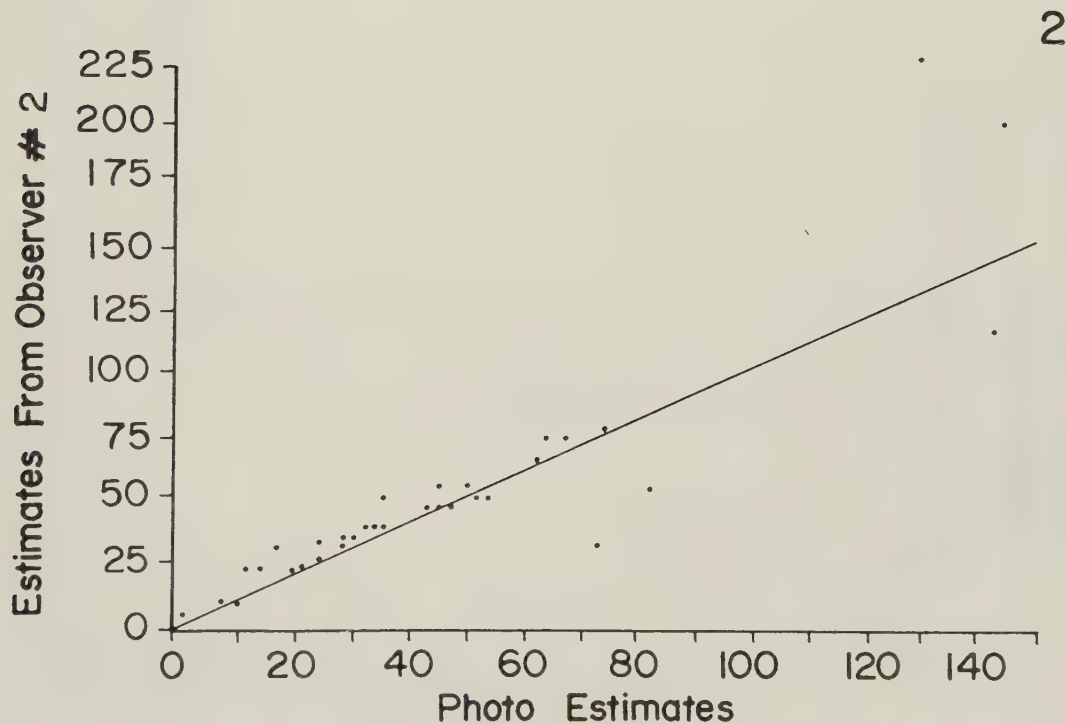
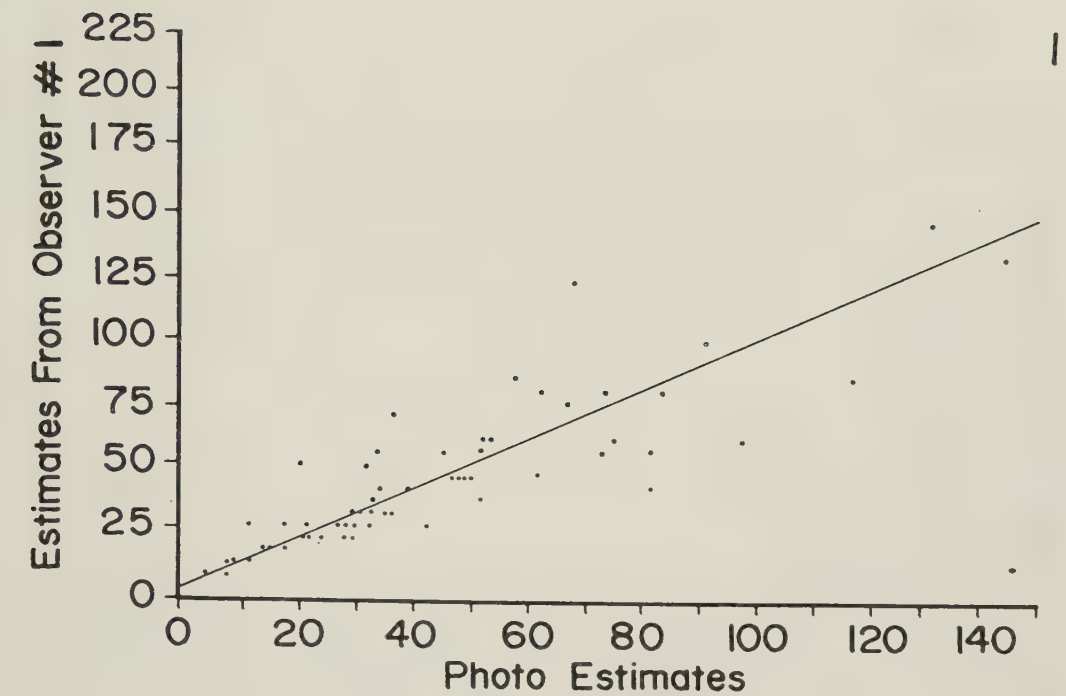


Figure 54. Comparisons of estimates of dolphin numbers per school:
(1) Comparison of estimates by Observer #1 and counts from photographs
(2) Comparison of estimates by Observer #2 and counts from photographs. The solid lines are defined by identical estimates from the two sources.

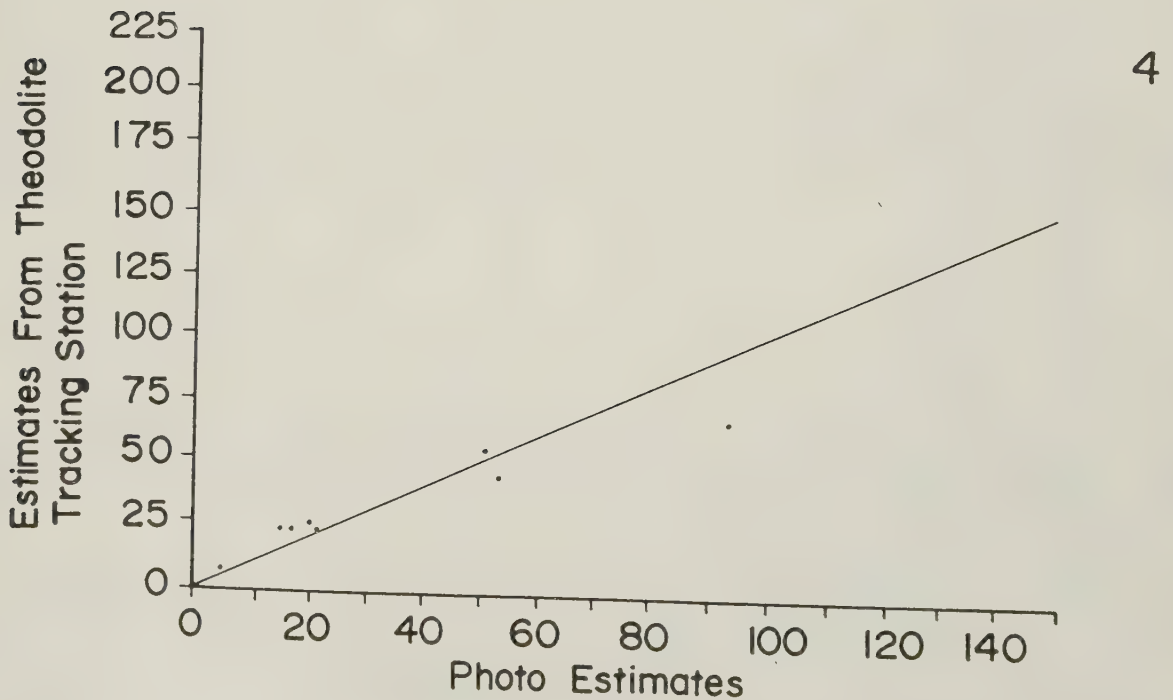
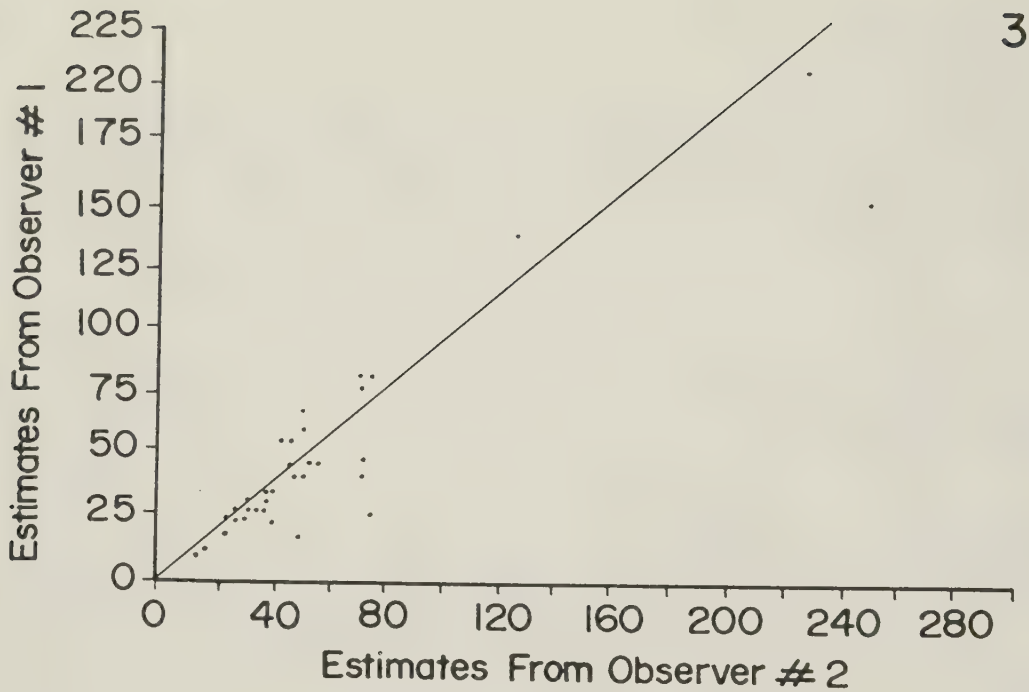


Figure 54. Comparisons of estimates of dolphin numbers per school:
 (3) Comparison of estimates by two aerial observers (4) Comparison of estimates by the theodolite tracking station to counts from photographs. The solid lines are defined by identical estimates from the two sources.

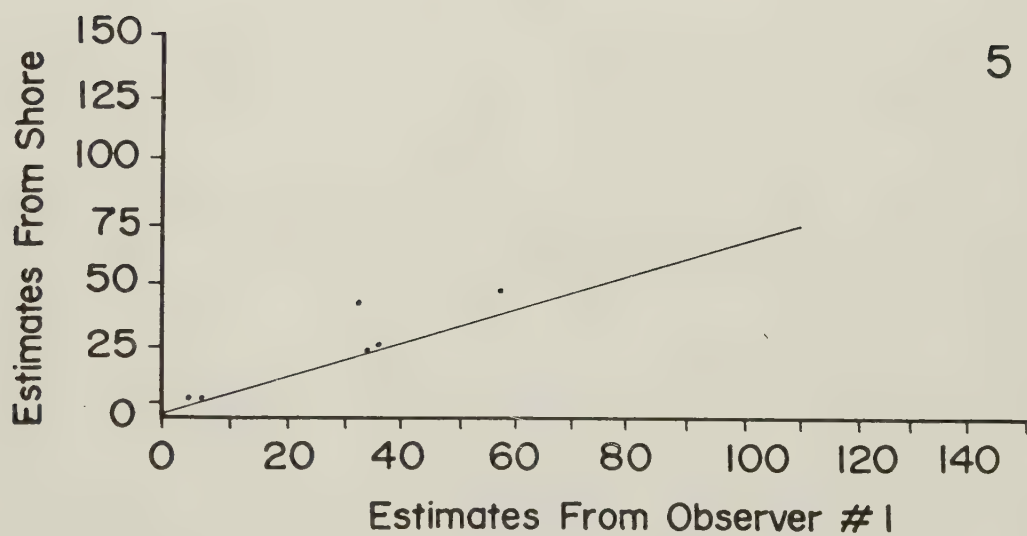


Figure 54. Comparisons of estimates of dolphin numbers per school:
(cont.) (5) Comparison of estimates from the Napoopoo shore station and aerial observer #1. The solid line is defined by identical estimates from the two sources.

movements of the school may be, and possibly that the tighter the school the less chance a predator has of singling out an individual (Norris and Dohl, 1980). Tight schools are probably also visual schools that come to rely upon close assessment of pattern marks and postures for instant information about a neighbor's intentions and hence the school can react with maximum swiftness to outside information.

With this model in mind, and after examining how spinner dolphins deploy themselves within their schools, we attempted to list the possible controlling features that may regulate the dynamics of dolphin schools. We arrived at nine "rules" that could be used to derive the school shapes and internal arrangements we saw. We do not always have proof for these rules, so further study is frequently needed. The model does, however, sharpen our perceptions.

These are the rules we derived:

(1) No animal, except a calf, may point its snout directly at the anterior body of another dolphin from a distance closer than about 15-20 m, except in anger. This results in similar orientation of animals nearest to each other.

(2) A "window" through the school envelope is almost always left open for the dominant sensory field of the moment (visual or acoustic) for each animal not engaged in close social interaction.

The visual field of individual dolphins involved both anterior and posterior sectors, and school echolocation is directed solely forward in a cone, extending both above and below the animal. The dolphins also possess a "cone of best reception" for sound (Au and Moore 1984), also directed forward. Parenthetically, the reality of this reception field was brought home to us when, lying in our viewing vehicle, or looking through the ports at Sea Life Park Oceanarium we produced clicks by tapping the ports when dolphins were near. This sometimes elicited scanning of the observer without any sound emission by the dolphin. Such a reception cone has been predicted anatomically by Norris (1968) and demonstrated neurophysiologically by Bullock and Ridgway (1972). Hence dolphin schools will have different internal arrangements and degrees of dispersion depending upon what sensory modality is dominant at the moment. In fact, these features are strongly evident between day and night.

(3) Associational behavioral sequences are arranged in temporally organized bouts (see Bout Behavior). These represent the major classes of activity of the school, and sufficient animals are usually present for individual school members to switch patterns frequently. This arrangement may limit the lower size of most schools (i.e. there have to be enough animals to fill all bout roles).

(4) The resultant patterns of all these features are modulated by a range of activity levels ranging from those of rest through awakening, travel, food search and feeding.

(5) The subgroups of a school can only maintain contact and cohesion effectively with a finite number of other subgroups dispersed in a finite volume of ocean; once again depending upon the main sensory modality in force at the time and its effectiveness. For a school depending primarily on vision about eight or ten subgroups and between 30 and 40 individuals seems about optimum. Above that number schools tend to fractionate into separate schools upon any significant disturbance. Our impression is that acoustically mediated schools may be much larger. These factors may relate to the upper size limit of schools.

(6) The number of dolphins per unit volume of water seems regulated in part by a balance of cohesive and dispersive "forces", at any one instant. These have been listed by Norris and Dohl (1980). For example, fear is a cohesive force that causes dolphins to press closer together. Frightened schools are dense schools, at least during the day when the visual modality is in force.

(7) Dolphin schools are obviously directed. They not only react adaptively to fear, or the need for rest, but they move long distances to feeding grounds and they return to certain rather small areas to rest. We tried to understand how such direction is imparted to a school. "Were there leaders?", we asked. "If so how did they impose their will on others in a school?" (see Leadership).

(8) Social structure has obvious effects on the distribution of the subgroups of a school

(9) Hydrodynamic considerations may be very important in how dolphins swim relative to one another. Almost always some degree of echelon formation is evident, and this may be the most energetically economical way to swim with schoolmates, just as it appears to be in some bird flocks (see Lissaman and Shollenberger 1970). It is also likely to be effective in maintaining open sensory windows for each animal.

In pages that follow we will discuss how these various putative determinants of school geometry seem to be effective in producing natural school formations. We sought to observe these processes directly, both in captivity and in nature.

But before these sometimes complex processes could be understood we first tried to understand the signs and signals used by spinner dolphins to mediate these processes. By signs we mean features of the animal's body form or pattern that carry meanings, and by signals we mean actions by an animal that carry meaning in various contexts. The first is inadvertent for the

sender, while the second probably often involves conscious participation by the sender.

Signs, Signals and Sensory Fields

Both sensory integration and social decision processes in the visual mode are doubtless heavily dependent upon various signs provided by the animal's pattern and form though we usually lack proof. For instance, many details of the dolphin's pattern seem useful in transmitting information about changes in body posture or attitude that will immediately result in changes in swimming direction. By closely watching each other spinner dolphins must know where adjacent schoolmates will move in the seconds just ahead. We will first consider sensory fields.

(1) Sensory Fields

Both signs and signals must sometimes be dependent upon the remarkable visual field of dolphins, which includes vision ahead of the animal, 180 degrees on each side and large fields both above and below the animal (see Figure 55). It is not clear how much of an overlap between the fields of the two sides of a dolphin there may be. In any event dolphins may be able to appreciate depth of field using a single eye at a time (Madsen and Herman 1982).

Some consensual movement of the pupil of the dolphin eye is produced by stimulation of the other eye (Dawson, Birndorf and Perez 1972). Madsen and Herman (1980) point out that a single dolphin eye may possess two fixed foci, one specialized for close up vision underwater, with a far point of one m or less, and a second focal point adapted for distant viewing, with a near point of 2.5 m or greater. This unusual state of affairs has been verified by Herman et al (1975) and is probably due to the opercular arrangement of the eye, which at high light levels produces two separate pupillary openings in a single eye.

These arrangements may also be related to the functions of the sensory integration system, and the tightening or dispersion of schools.

It also seems that the dolphin eye is movable in and out in the socket by engorgement or drainage of the ophthalmic rete behind the eye (Galliano et al 1966). Dolphin eyes may be raised on prominences above the general body contour or they may be flush with the contour of the head, both conditions possibly reflections of the level of such engorgement.

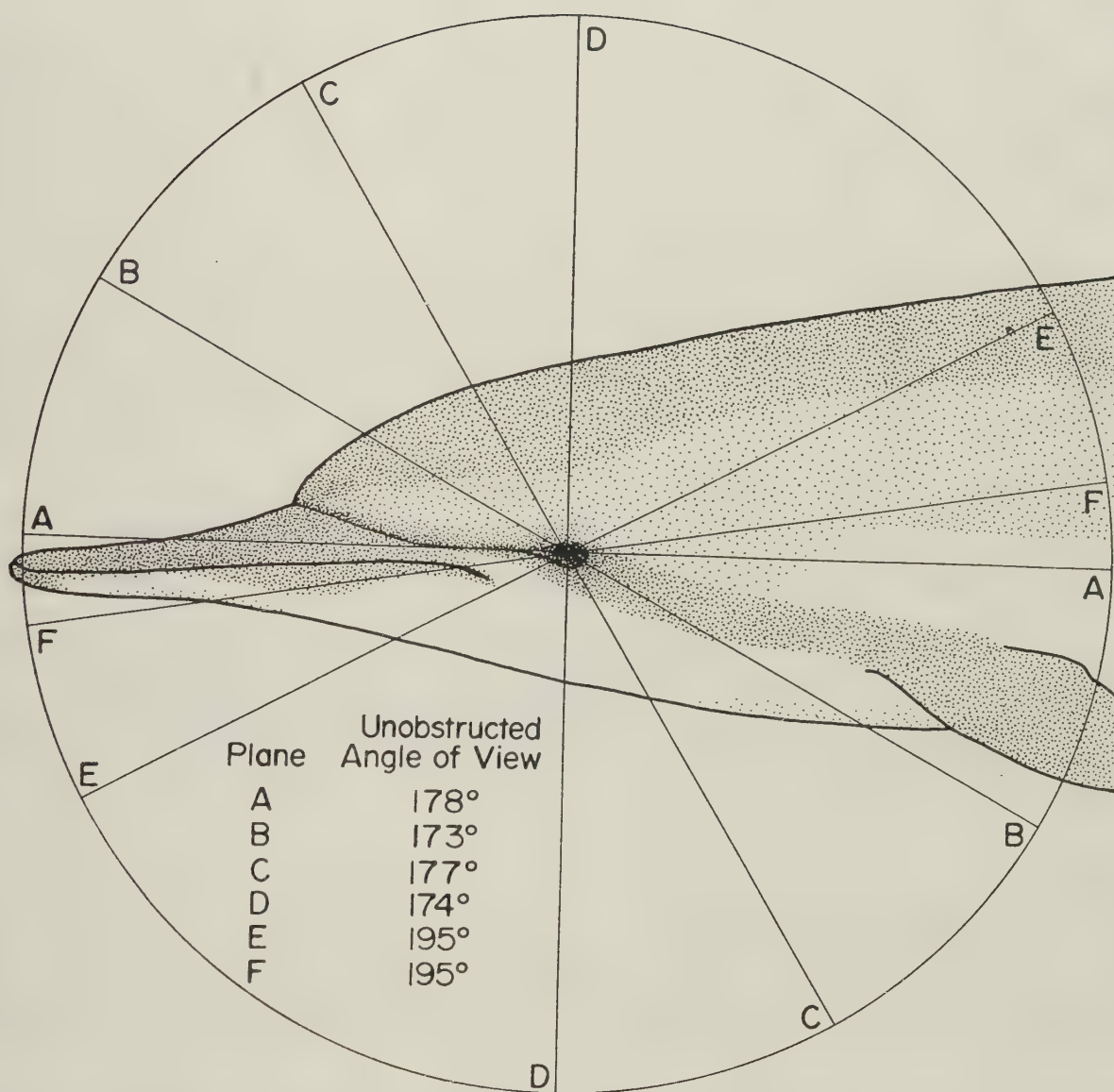


Figure 55. Visual field of the spinner dolphin at six planes.

The eyes of spinner dolphins are situated at approximately the widest point of the head, allowing the animal to look both forward and backward. This is enhanced by eye movement. One can sometimes see the eye of a spinner dolphin, raised on a prominence, cocked backward, forward or downward above the general body contour.

We attempted to describe the spinner dolphin visual field by describing the planes in which the pupil of the eye was visible from in front, behind, above and below an animal. To make these measurements we took the captive spinner dolphin Kehaulani out of water at Sea Life Park on Oahu, Hawaii.

In this spinner dolphin, the possibly slightly binocular forward field of vision above the level of the jaw did not appear to be as strongly developed as in the bottlenose dolphin. Visual angles relative to the body axis were measured using the outermost surface of the cornea as the apex of an angle described by lines extending from that point to the first point where the dolphin's visual field was obstructed by its own body. These lines defined the visual field of the dolphin in a given plane. The small angles in planes A-D are primarily a function of the supraorbital ridge that extends above and some extent anterior to the eye. It tends to limit vision above and ahead of the animal in regions covered by echolocation fields (See Figure 55). Larger visual fields were found in planes E and F.

An observer directly behind a spinner dolphin can clearly observe both corneas simultaneously, even when the eyes are essentially flush with the body contours. But an observer in front of the animal, looking down from above the jaw, can detect both corneas only when the eyes are protruded, presumably by retial engorgement.

2. Whole Body Signals

There are three other signals (a structure plus an action) we have learned to recognize from our film studies. These are belly-tilts, tilt-aways and belly-ups.

Belly-tilts (a tilt of the belly of one dolphin toward another) and tilt-away (the opposite rotation) are visual displays effective at very modest levels of expression. Even a slight tilt of the belly toward another, representing an axial rotation of perhaps 5 degrees, was predictive of continued or increased interaction between two animals, while a slight tilt of the back of one animal away from another clearly predicted a cessation of association. Such rotations of the body produce flashes of white or dark to a distant observer.

Only 41% of 366 observed belly-ups and 63% of 153 belly-tilts resulted in contact. Although poor visibility was great source of frustration to observers in the Maka Ala viewing chamber, the experience at such times of being able to see nothing but a glint of white from the belly of an inverted or tilted animal suggested the visual importance of these patterns. Few belly tilts were given without another animal in the immediate visual field (10%). The visual nature of these tilting patterns is emphasized by the countershaded pattern of spinners and the near vertical direction of incoming light when the animals are some distance below the surface. In fact the pattern gives rather precise angular formation to a receiving animal.

Belly-tilts occurred during the meeting of two animals, during prolonged pair swimming, in partner switches, and as a final display before two paired animals in a behavior bout separated. Considering the limited gestural communication available to these streamlined, animals such gross eye-catching movements are probably relied upon as general signals of recognition and acknowledgement.

An incident seen from the Maka Ala involving tilting-away is of special interest. It involved an animal rubbing its rostrum on another's tail stock and poking its flukes. The recipient animal tilted-away, righted itself and swam rapidly away. Often, in our motion picture analysis we have seen tilt-aways occur within triads, with a recipient animal being left as the other two animals engaged in a caressing bout. Such tilt-aways seldom elicited overt aggressive behavior from a recipient. The tilt-away may be an act that hides the white belly of one animal from another and/or places the protruberent dorsal fin between one animal and the next. It is also a position that allows rapid departure of one member of a tight group of dolphins.

Belly-tilts and belly-ups do seem to be linked in causal sequences that may sometimes lead to overtly sexual behavior. We note however that our assignment of sexual function is often our own and perhaps not that of the animals involved, since we came to feel that much apparently sexual behavior is, in fact, primarily communicative and not a direct part of the reproductive process.

However, belly-tilts are at times involved in tests of sexual receptivity between heterosexual pairs. We compared behavioral frequencies and serum hormone concentrations for captive spinners at Sea Life Park over a 14 month period. We found a significant relationship between the frequency of simultaneous or rapidly alternating belly-tilts (ventral presentations) and the occurrence of high concentrations of reproductive steroid hormones (Wells 1984).

From the standpoint of signal power the belly-tilt is a shorter and less powerful posture than the belly-up. Only about

one quarter (22%, n=211) of sequences in which at least one belly-up occurred involved other belly-ups or belly-tilts. But nearly half (46%, n=103) of sequences involving at least one belly-up involved other posturing. Non-genital contact was more often associated with belly-tilts (48% of tilt sequences; n=103) than with belly-ups (27% of belly-up sequences; n=211). As might be expected, belly-up sequences often lead to genital contact (24%; n=211). Conversely, in over half (56%; n=103) of sequences involving genital contact, there was first belly up behavior in a sort of fore play. It is interesting to note that every case (n=14) where belly tilting adults made genital contact they also turned belly-up as a precursor to such contact.

But, to put the belly-up pattern in its proper context, we note that in 76% of the 211 sequences with belly-ups there was no genital contact involved. This reinforces the idea that this pattern, and probably contact itself, need not necessarily be functionally sexual.

It is important to note that the Sea Life Park observations showed that genital-to-genital contact was associated with high hormone levels whereas other kinds of genital contact were not.

3. Pectoral Fins and Their Associated Pattern

The pectoral fin and flipper stripe (which runs from the anterior insertion of the flipper to the eye and posterior gape; see Mitchell 1970) of spinner dolphins are joined together as a single dark color unit that stands out clearly against the white of the throat and belly. Furthermore, because the flipper stripe is a fixed pattern and the dark fin is movable they together form a unit that can instantly indicate the degree to which the pectoral is swung downward from the body. The dark band composed of flipper stripe - fin is either straight as in the normal relaxed fin posture, or broken at an angle in the middle by the downward or forwardly flexed fin, as occurs during aggressive displays or during sharp turns then the pectoral may be thrust forward (Figure 56).

The pectoral fin notch, at the posterior insertion of the fin, also seems to provide information. In the relaxed position the notch is not evident, but when the fin is thrown forward, a round white space of belly color becomes evident as the fin pulls away from the body. This specific pattern component is found widely in odontocetes (Cephalorhynchus, Lagenorhynchus, Orcinus, Delphinus, etc; see Norris and Dohl 1980) probably because there is wide utility for one cetacean to know about the incipient movements or emotional state of its neighbor as told by the state of the pectoral fin.

4. Body Pattern

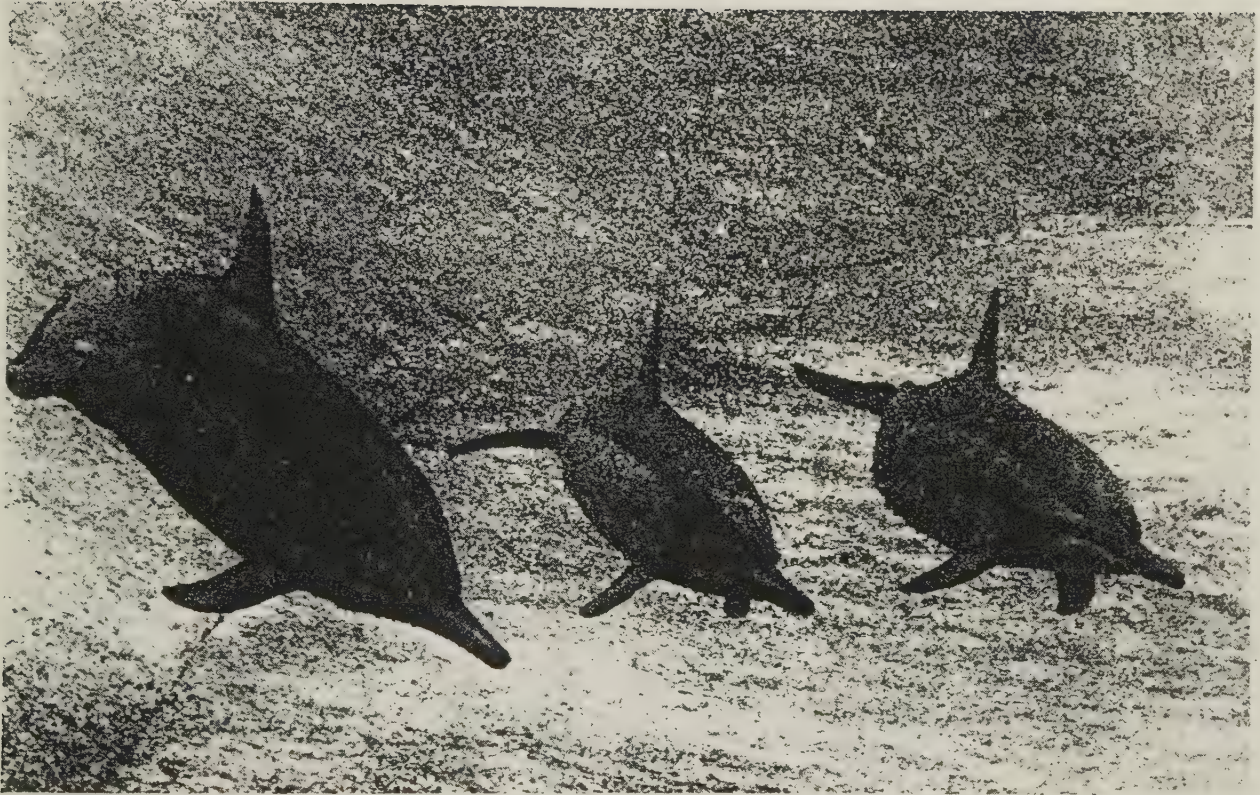


Figure 56. Formation swimming. Sea Life Park oceanarium.

The body pattern of spinner dolphins is roughly composed of dark gray cape (or the "spinal blaze" of Mitchell 1970), a lighter gray lateral field and white ventrum (see Perrin 1972a). The margins between these fields are apt to be sharply marked, or even enhanced by a darkening of speckles, as in the whitebelly spinner.

We suggest that the three major longitudinal pattern components allow dolphins to determine at a glance the degree of rotation of an adjacent dolphin. If the rotation is toward an adjacent dolphin the dark cape increases in prominence at the expense of the white belly field. It becomes more prominent if the animal rotates the other way. Such attitudinal relationships may be used as part of the system of cues that regulate synchronous turns, dives and surfacings.

The flash of bellies clearly indicates an active social state as far away as the signal can be seen, just as a more steady white reflection may carry the implication of rest or formation swimming.

The closer dolphins come together, the more effective such longitudinal fields should be for signaling. The sharp borders margining the lateral fields may allow some precision of estimation of the body attitude. The one meter focal length of the bottlenose dolphin eye mentioned by Herman et al (1975) may be related to the close inspection of such patterns by schoolmates.

5. The Rostrum

The dark rostrum of spinner dolphins seems to act as a pointer in school maneuvers, as we describe in the section on turning maneuvers.

The snout tip of adult spinners is jet black and in contrast to the white of the jaw tip of adult spotted dolphins. It is easy to discriminate these species underwater by this feature alone (Figure 57). It seems likely that this is a sign that may not only serve for species recognition but could emphasize the aggressive posture when one animal faces another (see Madsen and Herman 1980 for other signs). In the threat posture of spinner dolphins animals facing each other lower their heads and arch their backs. This movement has the effect of lowering the jet black snout tip over the contrasting white of the throat and thus emphasizing the posture.

6. Sexual Pattern

At the posterior end of the white belly of spinners the lateral field dips downward and ends in a pair of dark brush marks extending forward into the belly white above the genital

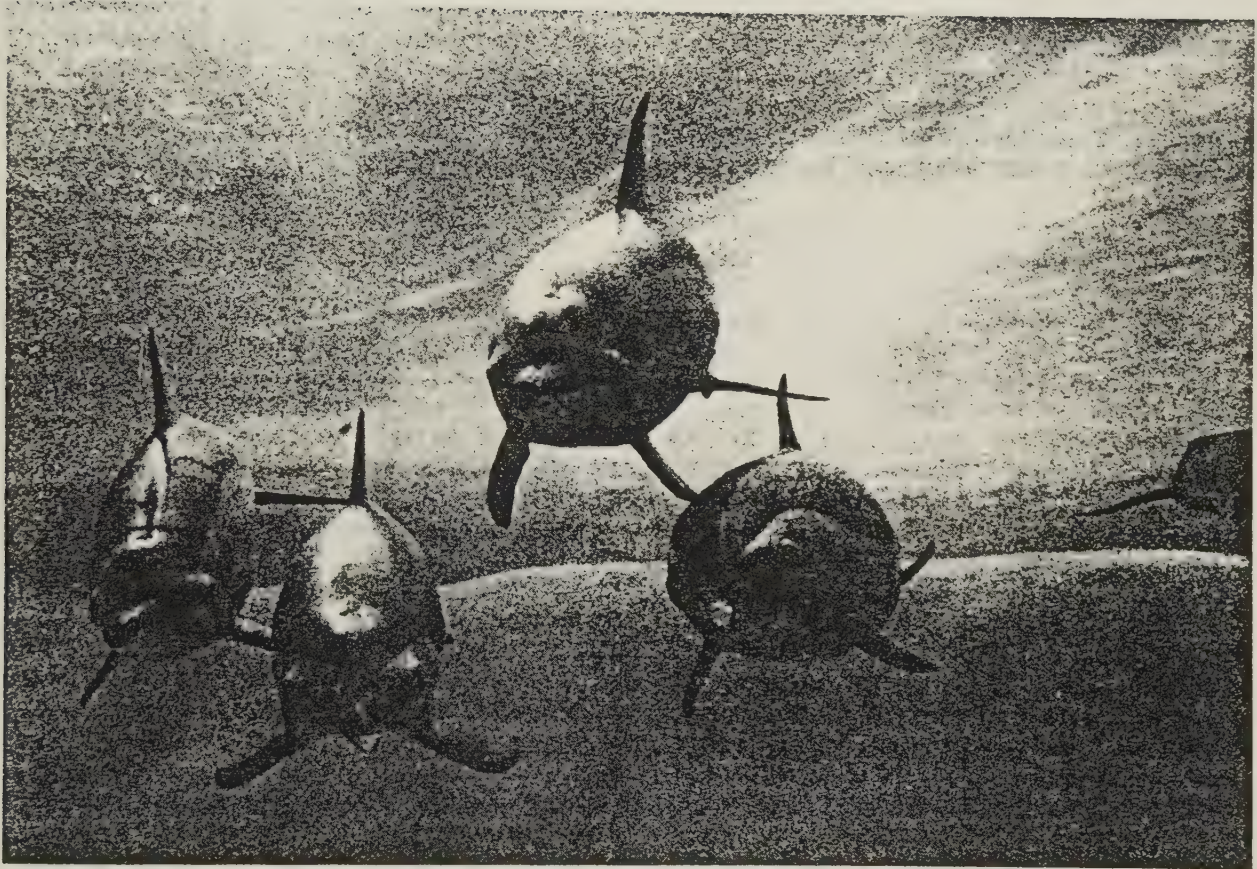


Figure 57. Pectoral contact by dolphins at Sea Life Park oceanarium. The dolphins with white beak tips are Pacific spotted dolphins, Stenella attenuata, and the black tipped animals are spinner dolphins.

region. And the ventral margin of the caudal keel may be light and extend into the tapering white belly. At this juxtaposition are located the anus and the genital slit, and somewhat further forward in males, the penial slit. As in most cetaceans such pattern marks serve to pinpoint the positions of these anatomical features with some precision. Both sexual and relational encounters in adults and nursing in young are doubtless mediated by them. Nonetheless, sexual dimorphism in spinners is modest, relating mostly to thickening of the tail stock, a moderate post-anal hump and an erect, tall and dark dorsal fin in males.

Having outlined signs, signals and sensory fields we may now discuss the various rules we derived for the determination of the shape and composition of dolphin schools.

Sensory Windows

If one examines the staggered arrangement of individuals in a dolphin school one can see that they tend to leave large portions of the available sensory field open through the school envelope. To be sure, when schools are very active, especially when caressing groups are found, some animals are in such close contact that inner animals must depend upon outer animals for environmental information. But, such groups never comprise the whole school. Group caressing tends to occur well within the school envelope.

For sensory integration to work optimally individual animals need to sense both outside the school envelope and from each other. The dolphins need to be able to sense and react to an approaching shark, and to transmit such information through the school. Such reception and transmission will involve the dominant sensory mode of the moment.

When Kealake'akua Bay water was especially murky, schools coming into the bay often left quickly, rather than settling into a rest period. We came to believe that the murky water prevented descent into rest. Since during rest vision is the dominant mode the murky water could be defeating its use in the mediation of sensory integration.

As for the acoustically mediated school, in which both sending and reception of signals is focussed forward, a different set of constraints on school geometry exists. The echolocation sound system penetrates the sea water under most conditions for at least 150 m, or up to perhaps 10X that distance depending upon the target size and reverberation (see Murchison 1980), allowing a school moving in the direction of sound transmission a great sensory advantage over any predator except another cetacean (such as Orcinus or Pseudorca, both of which are known to feed on dolphins at times; Perryman and Foster 1980). But the acoustic sense also leaves the rear sector untended unless the

echolocation activities of many animals are able to sweep these areas as the school moves along. This may be a task of animals engaged in echolocation bouts such as we observed in captivity, but we have no direct evidence.

Another method for dealing with such sensory asymmetry is for the school to retrace its path frequently. Feeding schools do seem to double back on their paths frequently and to traverse the water just recently scanned. A predator stalking such a school would have to swim faster than they do to overtake them from behind. The sea ahead is, of course, easily scanned. We should note that some evidence for shark predation on cetaceans does suggest the predominate approach is from behind, since flukes and tail stocks were the anatomical region most frequently bitten (see Arnold 1972).

Our frequent observation that very young dolphins were commonly in the lead of moving schools seems understandable since they swam in scanned waters.

Turning Maneuvers

Turning maneuvers were studied in two ways. First, they were determined by frame-by-frame analysis of underwater moving pictures, and second, they were observed in the captive school. In captivity one could watch the shadows cast on the tank bottom by animals swimming above and often perceive easily which animal had turned first.

In undisturbed schools, turns were almost always initiated by adult animals, apparently of either sex. Such turns seemed to come preponderantly from the outside or lower portions of a school, and often from behind. The initiation of the turn process consisted of a single animal bending its anterior body and snout away from the line of travel, with adjacent animals then responding. Such signals were so slight and subtle as to require careful scrutiny, even in frame-by-frame analysis, to determine which animal had initiated the turn.

As the initiating animal turned its snout and began to diverge from the path of the others, others followed by bending in the same direction and then the whole school might follow. This movement then might influence other nearby subgroups in a scattered school until the entire school envelope had reoriented.

Acoustic signaling may accompany such turns. In the captive school we sometimes heard a rather low intensity two-parted click given when an adult male spinner initiated turns. A turn sequence is shown in Figure 56.

Our conclusion is that there is not a single school leader in the sense of an animal leading the way with others following.

Instead, turns are made in a dynamic three dimensional fashion, starting from any sector of the school, probably usually initiated by the more experienced animals. One suspects that under conditions of stress any animal reacting to a sufficiently strong stimulus could initiate a school turn, especially if supported by other animals in the vicinity reacting to the same stimulus. In this fashion incipient predation, for example, could override the normal leadership function of the adult cadres within a school and turning instructions could come from any age class.

In either the normal undisturbed school or in one under stress the transmission of information involves sensory integration. This mechanism is essentially the same as that regulating the movements of animal groups as diverse as gnat swarms, krill schools (see Hamner et al 1984), bird flocks (see Davis 1980) and antelope herds. It is dependent upon the rapid transmission of positional information in three dimensions. It operates between schoolmates using the dominant sensory modality of the moment and the system of signs and signals of the particular species.

In the case of dolphin schools, when a peripheral adult turns its head toward inner schoolmates they do not allow the disruption of having the snout pointed toward them to proceed very far before they turn in the same direction and reduce the discontinuity. The snout of the spinner dolphin, seen from above or from the side, is a slim black pointer and seems to be used as such. In film analysis we came to realize that adult dolphins almost never point their snouts at each other, and even modest deviations have much signal value. Most turns were initiated by mere feints of just a few degrees. Only when a turning animal swam out of the plane of the nearest animal was the snout of a turning animal allowed to deviate as much as 30 degrees from the path of a partner. And, we came to believe that such pointing of the snout also carried a strong negative or aggressive connotation in individual exchanges between animals.

We came to wonder, but can bring no direct evidence to bear upon the question, whether pointing might be a threat because the pointing animal was at the same time threatening to direct sounds at an especially vulnerable sector of the animal's head, which could do serious damage to the crucial hearing mechanisms.

It is interesting to reflect that time and time again as we watched schools from our viewing vehicle or when we swam toward them, subgroups of adult males interposed themselves between us and the remainder of the school. They became the watchdog group that, should we make a feint toward the school, would react by turning. As a result, the full power of their status was imparted to their decision to turn.

Calves routinely violated adult rules in the matter of snout pointing, often approaching adults at angles of 35-60 degrees. Thus it is clearly part of the maturation process to conform to

adult rules, and at the same time, to take a position in the adult cadres of the school where snout deviations have signal meaning, and come to be effective in directing the school.

Episodic or Bout Behavior

After concerted observation of a trio of nearly undisturbed captive spinners it became obvious that, much of the time, the behavior of a given animal was arranged in periods, or bouts, in which a single behavior pattern was pursued. These bouts ranged from a few minutes in length to more than half an hour long.

During a day an animal might alternate between bouts of click train emission, caressing, aerial behavior and group swimming. This strong tendency we called 'bout behavior'. We also came to realize that the bouts were real entities because the animals engaged in them did so with marked singleness of purpose, and because these bouts had recognizable beginnings and ends. They began, built in intensity, and then subsided. Terminations were times of clear oscillation between the pattern at hand and the new pattern about to be performed. Each of the pair of animals had a clear role. In low intensity caressing, for example, there was usually a caressor and a caressee throughout the entire bout.

To make these relationships graphic for the reader we will describe a single bout and its termination. The example is a composite from observations of the captive school at Sea Life Park.

The two adult female spinner dolphins, Kehaulani and Kahe, have come together in a caressing bout. Kahe reaches out toward Kehaulani with her inside pectoral fin tip, running its anterior edge and top over much of the latter's body, especially between the pectoral fins, along the abdomen, and onto the genital area. Kehaulani solicits these caresses by swimming up next to Kahe, or turning under her so that her belly and sides are slowly run past the outstretched pectoral of the caressing animal, while they both swim forward. The caressing animals's outside pectoral is in normal swimming position, and the reach-out by the caressor is thus made obvious.

As the bout proceeds, caressing becomes more and more constant and intense. Swimming speed increases. One can see that Kahe extends her pectoral in synchrony with the undulating swimming motions of the recipient, extending and retracting to maintain contact, and then pulling away as Kehaulani speeds, sweeps past, and circles in for further contact. This period of increasing contact consumes 6 minutes.

Contact has become intense and the partners are in close juxtaposition much of the time. This state persists for 10 minutes, with the two animals attending only to each other, swimming together and circling for new position adjacent to one another. Then, both the intensity of contact and its frequency begin to diminish.

Kehaulani breaks away, races to the bottom of the tank, vibrates her belly and genital area against the bottom, and then bursts from the water in a spin. She reenters, and returns to Kahe to resume receiving caresses.

The degree of contact in the next 10 minutes clearly begins to oscillate slowly between close caressing and more distant behavior in which one of the extended pectoral fins of the caressee are stroked by Kahe (Figure 57). With experience the observer knew that the bout was nearly at an end.

Kehaulani drifts out of contact with Kahe as the pair circles, but she continues to swim alongside her for 60 seconds before drifting back into a closer position again, receiving body caresses for 20 seconds before drifting apart again, out of contact and this time with full body diameter separating the swimming animals.

The animals drift into contact again, this time for only 10 seconds, and drift out to pectoral tip touching distance for 10 seconds, and then swim alongside one another with a full two body diameters between them. This persists for 30 seconds.

They come into contact again, this time for just 3 seconds before drifting into the more distant formation swimming again. The synchronized pair approaches the male Lioele, and the partners go on opposite sides of him, and instead of coming together again they circle in opposite directions. Kahe assumes a position alongside the male while Kehaulani races to the tank bottom, rubs and vibrates her belly on the bottom and then bursts through the water surface in a high intensity spin. She continues to spin alone for the next 20 minutes while Kahe and Lioele swim together.

We later found that Purbrick (1977) had observed a similar cyclicity in a larger captive spinner dolphin population though she did not describe the patterns in detail.

The discovery of this temporal patterning led us to look for such sequences in nature. We sought to determine if in nature a single animal repetitively performed a single pattern. We did find such sequences for aerial patterns that were easy for us to observe. We also found caressing bouts to occur. The difficulties of prolonged field observation of individual dolphins made it impossible to define the durations of bouts in nature with any precision.

The small size of our captive school automatically highlighted such repetitive patterns of behavior. For example, in a three animal school if two animals caressed, the third was left alone to do a different, single pattern, and patterning was thereby imposed on their behavior.

Nonetheless, even though many animals were always available for interaction in wild schools, we still found single animals repeating aerial patterns over and over, and we were sometimes able to describe fairly extended caressing sequences involving three individuals (Figure 58).

In captivity such bouts were superimposed over, and in part overridden by, the diurnal behavioral sequence. That is, while in active periods certain animals could be observed in behavior bouts such as caressing, click train emission or aerial behavior, when the rest period came such bouts were suppressed in favor of formation swimming, which is the typical pattern shown during daytime rest.

Investigation of bout behavior in wild schools seemed potentially important to us because it could, if found, represent the means by which a traveling and diving school of dolphins partitioned out the essential patterns that allow the school to function. It could be the design of a division of labor. The spins could mark school shape and boundaries, the clicks protect and find food, and the caresses reaffirm relationships in a school in which learned patterns were predominant.

If spinning and other aerial patterns serve to define the position of a given dolphin for schoolmates as we suggest they might, and hence in aggregate define the envelope of a school for its members, then such patterns must be performed in all active schools with sufficient frequency to be useful.

And, if click train emission serves the general school maintenance functions of food-finding and location of predators it too should be both widely distributed spatially and relatively continuous in active schools.

The overall occurrence patterns of both aerial behavior and click emission fit these criteria. That is, both were widely and continuously abundant in active schools. We will now describe each of these "bout" patterns as we were able to define them in captive animals, and we will provide such field observations as we were able to obtain.

(1) Aerial Behavior Bouts

Aerial activity patterns and their relation to the diurnal cycle are described under Aerial Behavior. Here we deal with their organization into bouts.

SOME TYPICAL PARTNER RELATIONS

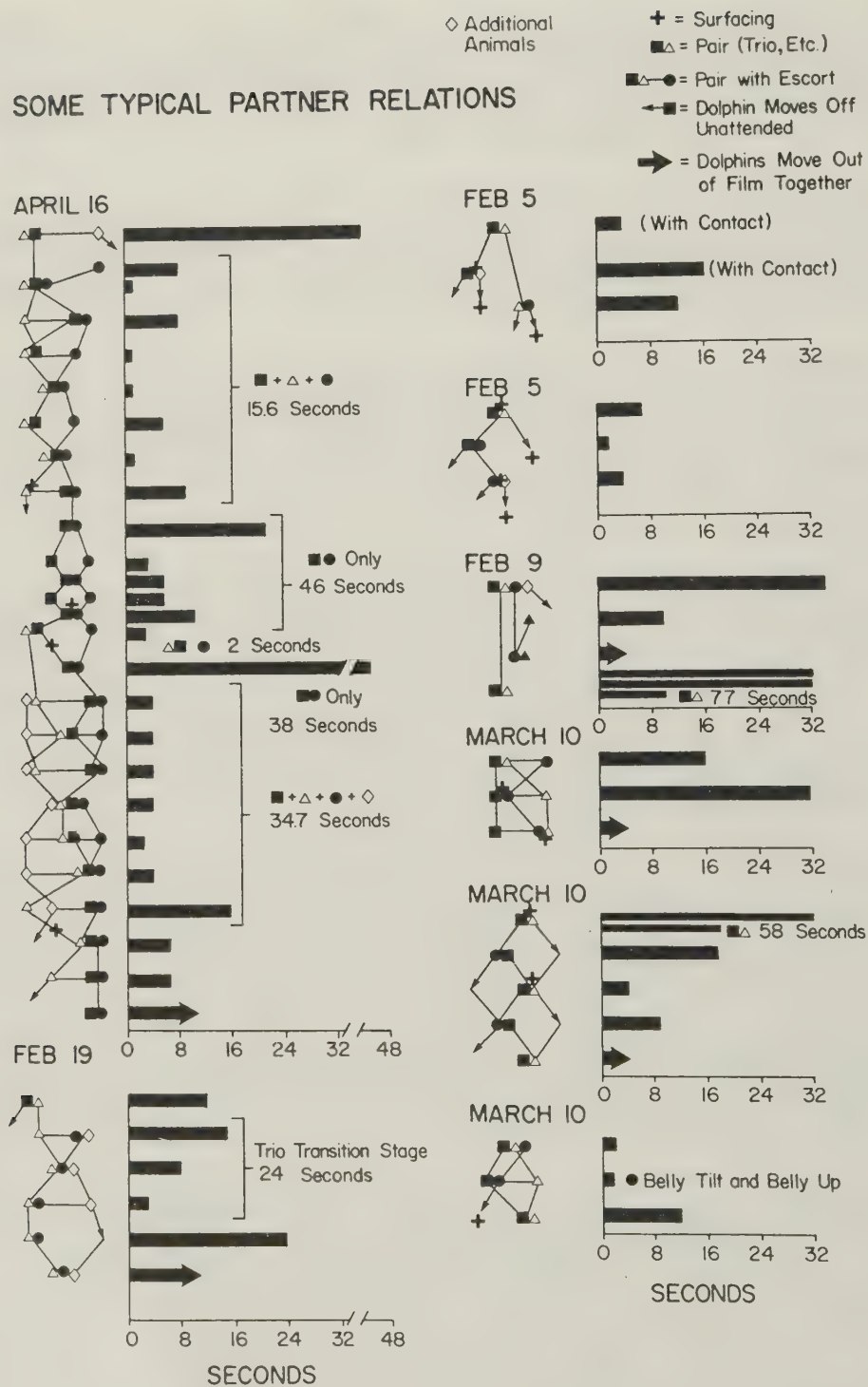


Figure 58. Examples of partner relations from five days of underwater observations. Note that most changes in pattern occur upon surfacing.

Spins, observed both in nature and in captivity, are given in series, sometimes for relatively extended periods (Table 3).

Usually a spin series seen at sea starts with high energy spin and is followed relatively rapidly by a series of spins by the same animal. These usually decline in intensity as the series proceeds, until the last spin may not clear the water. Once such a series is complete it is usually difficult to determine whether or not the next sequence in the same general area is performed by the same or another animal. Nonetheless, one sometimes felt reasonably sure that the same animal performed sequence after sequence of aerial patterns because of its size, its location within the school, or special features of its spins.

One feature provided the strongest evidence of such long series or bouts. Spinner dolphins typically do not mix the various kinds of aerial patterns in single sequences of aerial activity. Spin sequences do not contain tail-over-head leaps or head slaps. Further, aerial patterns are given in different ways that may be idiosyncratic to the individual. Some spin sequences were repeated by the same animal over many minutes time.

The numbers of leaps in a single spin sequence ranged from single spins to about 20 spins, and the average was about 3 or 4 spins per sequence. But we are not able to present exact numbers because we usually could not be absolutely certain that the same animal was responsible for all spins of a sequence.

Spin series give the impression of being given with intensity and singleness of purpose. To illustrate, while we traveled with an evening feeding school we noted an animal spinning rather close to the boat. One sequence of spins began some distance from the starboard bow, and each spin brought the animal closer to the boat. The final spin of 14 spins was so close that the animal reentered into our bow wave, startled and swam rapidly away.

(2) Caressing Bouts

In our captive observations these bouts between two individuals tended to be fairly extended, ranging from 9 to 30 minutes in length. As noted earlier we could not be sure of durations in nature, but we have observed bouts that lasted only a few seconds, and others, with four animals participating, that lasted for several minutes (see Figure 58). Clearly enough, the presence of several animals in the immediate vicinity of a caressing pair tends to cause a continual testing of the strength of the bond between the two animals and results in frequent switches between partners and other animals.

The higher the activity level of a school the shorter the attention of one animal specifically to another seems to be,

often finally giving way in high energy schools to group caressing where specific partners are difficult to discern, if in fact they exist.

Group caressing is very active behavior involving what seem to be entire subgroups within a school. As the animals swim along they move into close juxtaposition with one another and begin to weave amongst one another in frequent contact with more than one animal at a time. Such groups form tight fluid pods of animals in which much twisting and turning is evident, even to the fairly distant observer, because of the constant flashing of white bellies that can be seen, often from three or four animals at once. Doubtless this flashing signal is evident to the animals and may draw animals into such groups.

Both in nature and in captivity all available combinations of sexes and ages from very large calves to adults of both sexes take part in any combination. Tiny calves in the company of their presumed mothers were sometimes involved in caressing bouts.

Caressing itself involves rubbing a partner with pectoral fins, or flukes, pectoral whetting, bodily contact often in the mating posture in group caressing, and more passive patterns in which one animal may propel another through the water with its rostrum.

During what we presume are oestrus periods more active mating patterns and intromission became frequent. Wells (1984) found a significant relationship between high reproductive hormone levels and high frequency of genital-to-genital contact in captive spinners.

Caressing occupies a considerable part of a dolphin's day. While it does not occur during true rest periods, in active schools in daylight it is usual to see 30% or more of a school engaging in caressing patterns. Judging from observations of captives these patterns continue through the night.

Other very clearly defined caressing patterns were noted. The most unusual was beak-genital propulsion (Figure 59). In this pattern an upper animal "invited" a second animal to come up from below it, and to place the tip of its rostrum in its genital slit. The lower animal often turned partly on its side sometimes supporting the horizontal flukes of the upper animal across from its head to its outstretched pectoral fin. In this position the lower animal, its tail bent down slightly from the horizontal, propelled the upper animal forward, only breaking from the pattern to rise for breaths of air. Sometimes it swam belly up or dorsum up during propulsion.

Because of the unique position of the animals, and because of the possibility that clicked sound may be projected from the

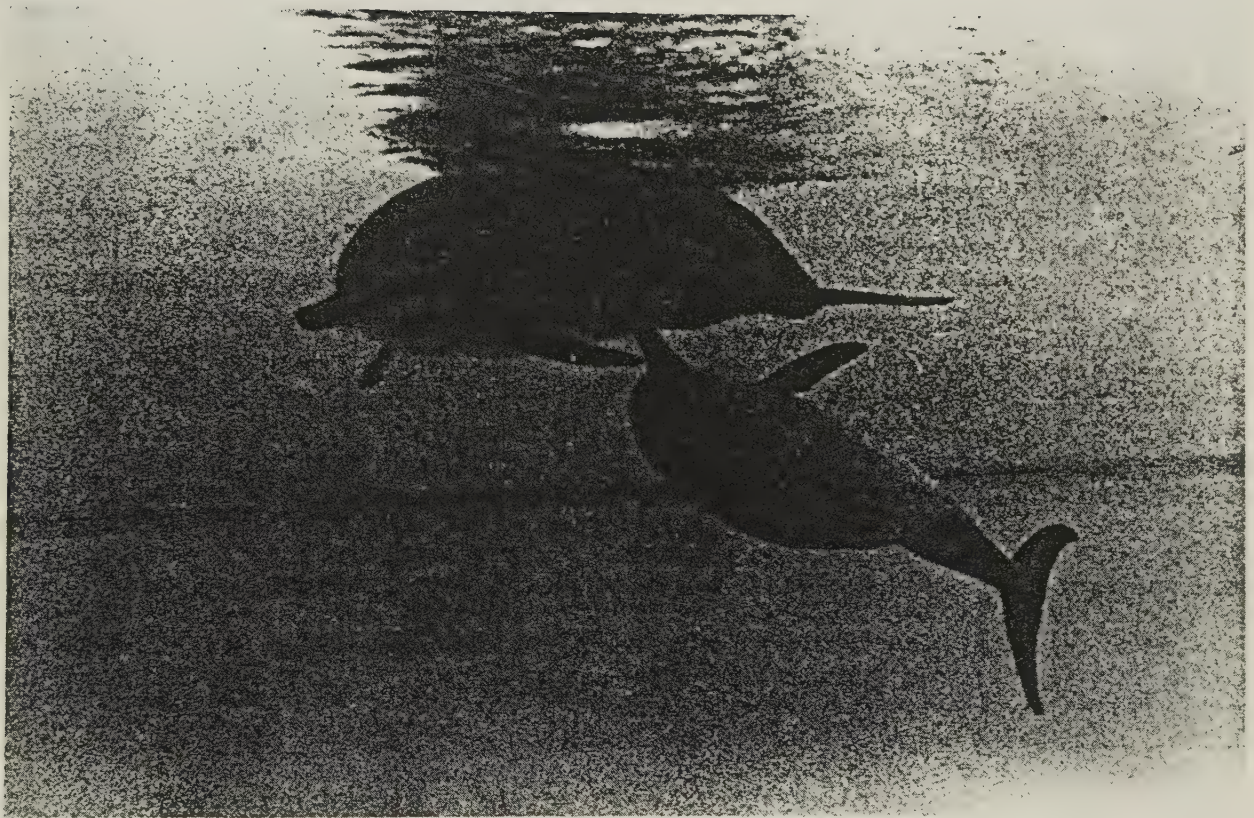


Figure 59. Beak-genital propulsion by captive spinner dolphins; Sea Life Park oceanarium.

rostrum of the propelling dolphin, we wondered if the behavior was accompanied by acoustic stimulation. Though we were several times able to hear low level clicks being emitted while this pattern was in progress we could never be sure which animal emitted the sounds, nor could we see any evident reaction by either animal.

This pattern was first described by Bateson (1974) and illustrated by Norris and Dohl (1980). It is a low activity level caressing pattern in which we never saw partners or their roles change throughout the bout.

A more active pattern is pectoral whetting. It has sometimes been seen by us during active school movement. In this pattern one animal swims inverted under another. The pectorals of each are scissored rapidly back the forth over the surfaces of those of the other.

(3) Formation Swimming

Formation swimming is a low energy pattern seen only in resting schools during the day. It is typified by sedate movement of subgroups of dolphins out of contact with one another, and with about one to three body diameters intervening between the pectoral fin tips of the animals. The pattern is represented by a range of expression. At its most sedate the subgroups within a school tend to become muted as the member animals become spaced fairly uniformly in groups as large as 20 animals. Looking from above, as we often did from our viewing vehicle Maka Ala, one could sometimes see their groups moving slowly over the sandy ocean floor, the animals side-by-side. We came to call this deep rest arrangement a "carpet formation" (see Figure 60).

In more active states of rest, subgroups become more and more evident but the animals continue to move sedately, and nearly silently, out of pectoral contact with one another. Not until arousal begins does one note caressing patterns. The view from above, even if animals could not be seen clearly, was of pairs or trios of animals, one of which flashed the white of its belly as it tilted toward its partner. Close observation showed that the same sort of oscillation as seen in captivity occurred, even though apparently taking place very much more rapidly. Trades between caressing partners became frequent (See Figure 58).

(4) Click Train Bouts

The following is a description of this solitary behavior as observed in captive animals. A lone dolphin circled the tank while directing loud high repetition rate click trains at various tank features. The dolphin circled very close to the bottom



Figure 60. Spinner dolphins in "carpet formation" over shallow sandy area of Kealake'akua Bay. Note adult males in foreground.

and tank walls. As it passed over cracks between cement slabs it often swam along these features emitting such trains. When the dolphin passed over the central drain box, which was a rectangular depression about a meter square, in the center of the tank, it paused and directed train after train of whining clicks into the dark space.

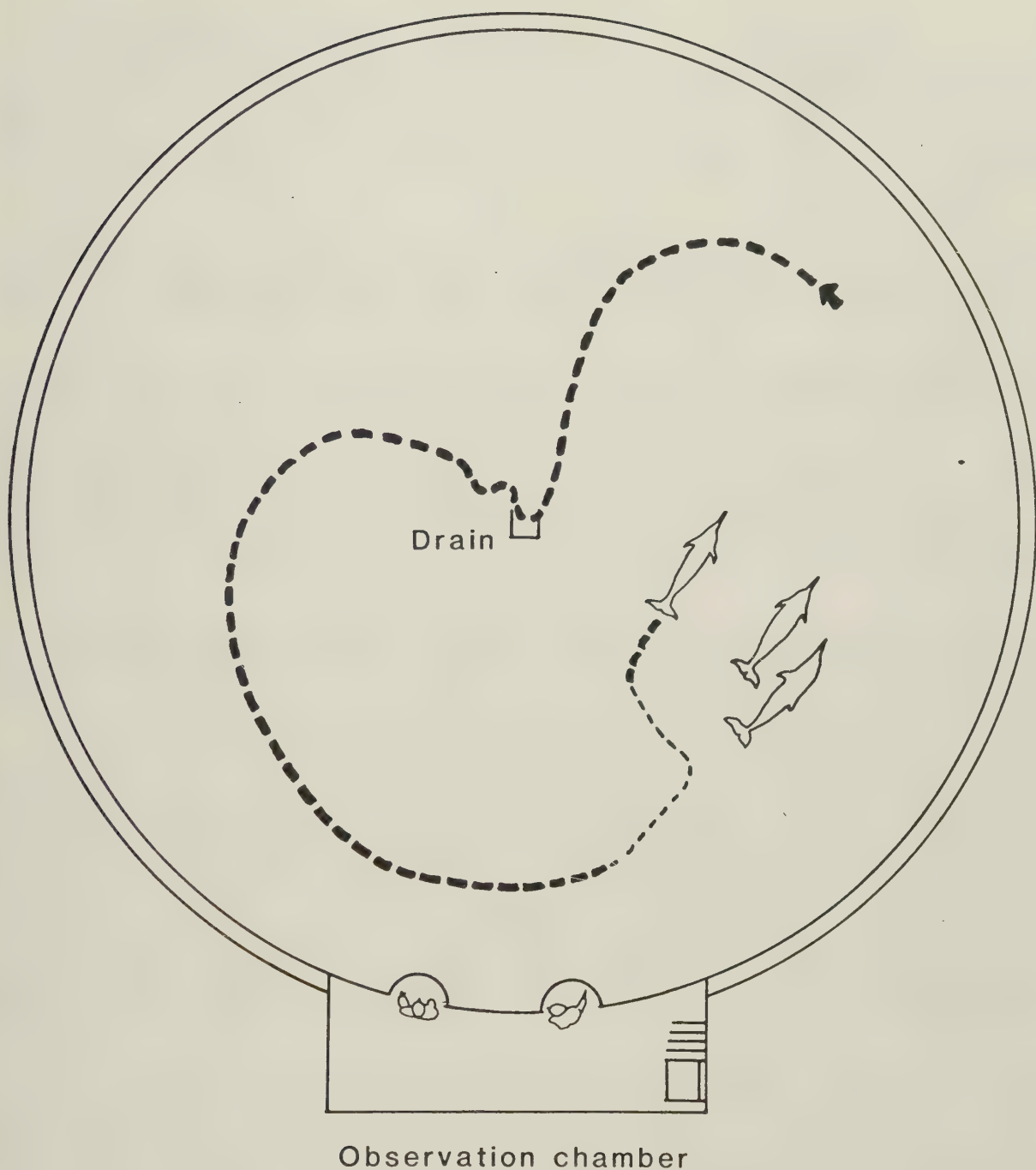
Click trains bouts were moderately long; the average for five bouts was 27 minutes (range 15-46 minutes).

We wondered if a clicking dolphin would direct such click trains at other nearby dolphins. We found that in general they do not. In fact such clicking dolphins proved to be remarkably solicitous of their tankmates. For example in the three dolphin school a dolphin was observed circling the tank in an echolocation bout. Each time it circled it came up behind its tank mates, and in each of 50 successive passes it either contrived to swim below them if they were near the surface, and continued click train emission, or if they were deeper in the water, shut down its clicking either to silence or to a very faint trains, and at the same time very obviously turned from their path. Once on a different path it quickly recommenced loud train emission. We came to call this "echolocation manners" (Figure 6)].

The reader should not conclude from this that dolphins never click at each other. Low level clicks are apparently directed between animals during caressing bouts in what we anthropocentrically called a "tickle buzz". These were soft sounds very different from the whining crescendo of echolocation click trains. As we noted elsewhere, a small burst of clicks, often only one or two, emanate from schools during the process of turning. And we later describe double clicks of high intensity that are used aggressively.

(5) Partner Sharing and Exchange

On September 16, 1980, a school of four dolphins was followed for 101 minutes as it traveled between two points of land about 200 m from shore, south of Kealake'akua Bay. The school was the smallest we monitored during our entire study. It was composed of two large adults, both with high triangular dorsal fins (Figure 62, #26 and #165), an adult with smaller, more falcate dorsal fin (#87), and a three-quarter grown subadult (#152). The first two animals, with tall fins, were typical of ones we came to regard as adult males. Such animals frequently travel in subgroups within a school, and have been described by Pryor and Kang (1978) for the spotted dolphin, Stenella attenuata. These authors found such adult male groups to patrol through school of dolphins trapped inside yellowfin tuna seines. Such groups are commonly observed in Hawaiian spinner dolphin schools, and usually interpose themselves between the school and the observers (Figure 1).



Observation chamber

Figure 61. Typical traverse of a spinner dolphin during an echolocation bout. The heavy dashed line shows path of the dolphin when emitting regular loud echolocation trains. Light dashes show animal coming up behind a pair of dolphins and shutting down its echolocation, turning sharply away from the path of the other dolphins and beginning to echolocate again.

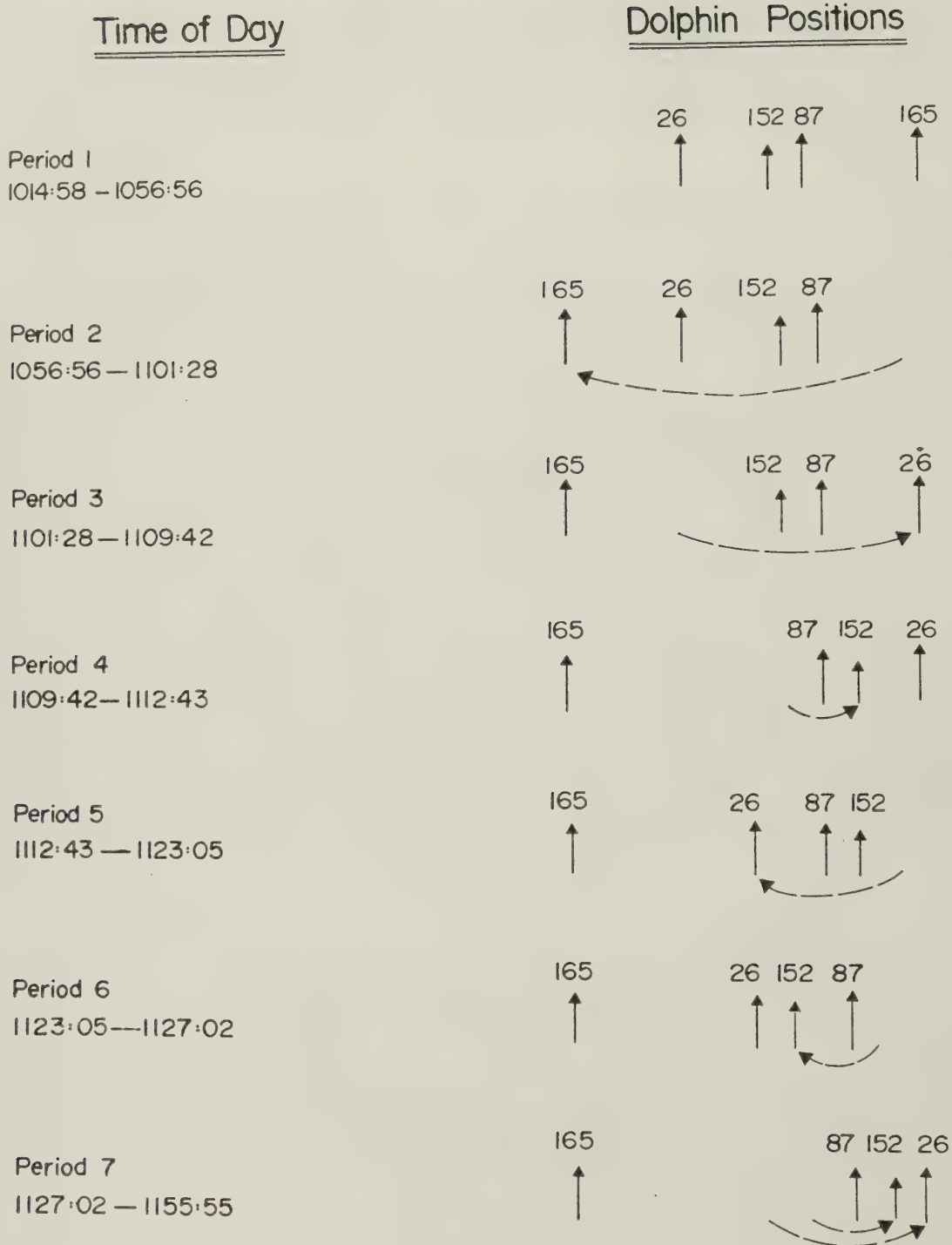


Figure 62. Relative positions of four dolphins traveling together, Kona coast, September 16, 1980. Animals 165 and 26 were perhaps adult males, 152 was a juvenile, and 87 a small adult. Periods were defined by changes in relative positions.

The adult-young pair could have been mother and young but we were unable to determine the sex of either. Suffice it to say that they stayed rather close throughout the entire encounter, especially so during the first part of our series. With one exception, the juvenile was interposed between the two presumed adult males.

The association between the juvenile (#152) and one of the presumed males (#26) became ever closer during our observation. But at the same time the juvenile maintained its close association with the small adult that could have been its mother (#87).

Proximity seems to have induced synchrony of surfacing even if the animals were not directly adjacent to one another. In other words there is a clear cohesion shown in our statistics. For example, #165 swam in rather close association with the other three dolphins during the first 40 minutes but swam alone and was usually separated by more than 8 m from the others during the latter part of the encounter. It frequently moved within 4 m of the others but did not join them, nor was it joined by the others.

The closer animals (less than two body length apart) showed their close association because they tended to surface together (scored when dolphins surface within two seconds of each other).

During the first 56 minutes when dolphins were mostly within 4 m of each other, 140 of the 229 surfacings were made synchronously while in the latter 45 minute period the association loosened and only 32 of 272 surfacings could be called synchronous (the difference was highly significant; chi-square= 134.4 $p < 0.001$). Perhaps at the start of observations the dolphins were afraid of the 5 m inflatable vessel and became more accustomed as time went on. The juvenile occupied the side away from the boat. Then as time went on the school began to loosen somewhat and the synchronous surfacing became less evident. The boat moved at constant slow speed throughout, matching the pace of the dolphins.

We could occasionally see behavioral signals. We saw both #87 and #26 tilt their bellies toward #152 twice during the latter half of observations. Once we saw #152 reciprocate, tilting toward #87, and then the two swam on their sides with stomachs touching for about 10 seconds. Surfacing patterns were instructive (Figure 63). During the first five observation periods the juvenile and the small adult surfaced almost completely in synchrony, but even when later on they did not, there remained regularity in the way the two individuals surfaced. From 10:39 to 11:03 the small adult surfaced just before the juvenile on all five asynchronous surfacings, and these were interspersed among numerous synchronous surfacings. And then from 11:05 to 11:12 the situation was reversed, and when asynchrony occurred the juvenile surfaced first until the end of

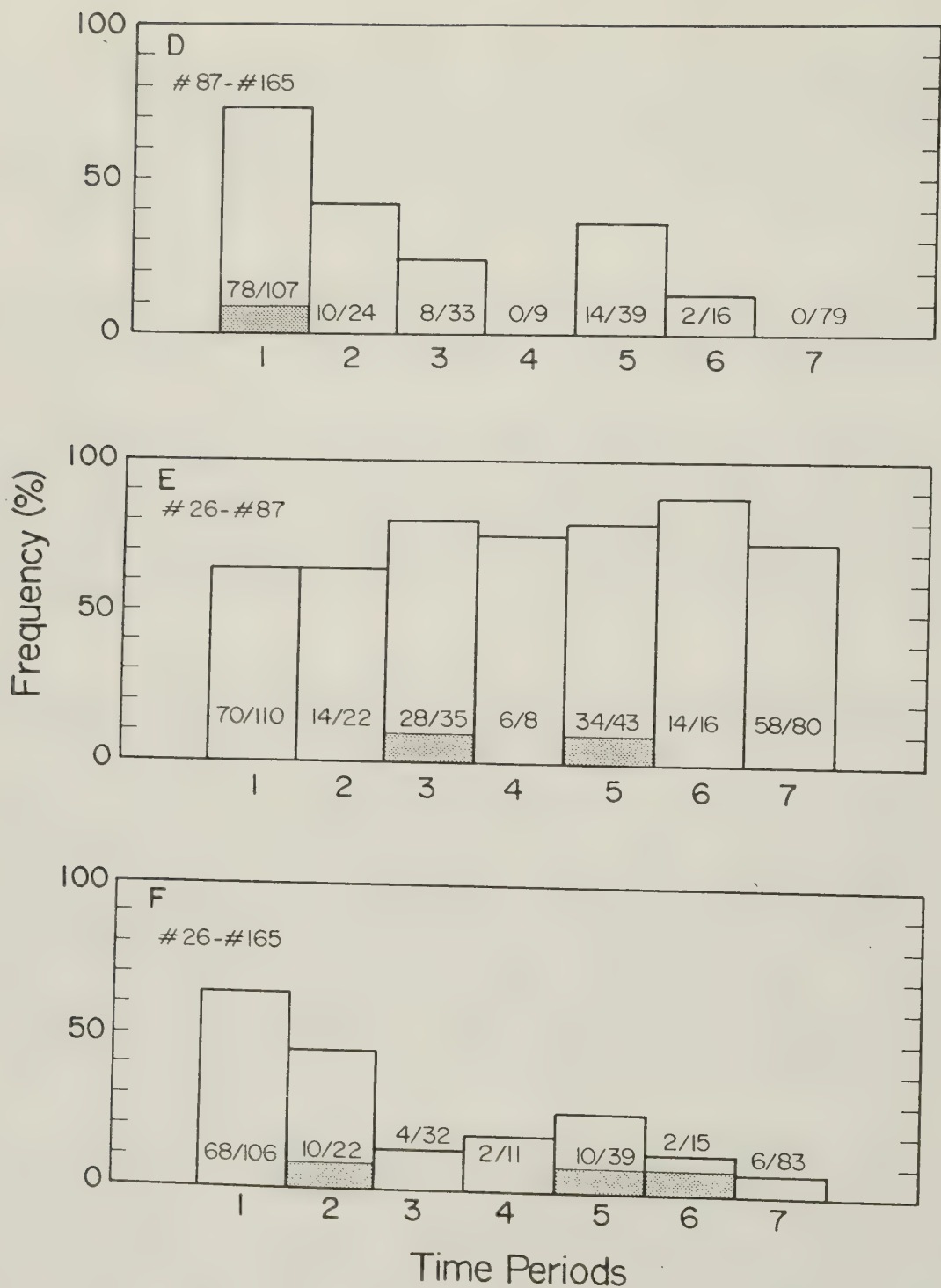
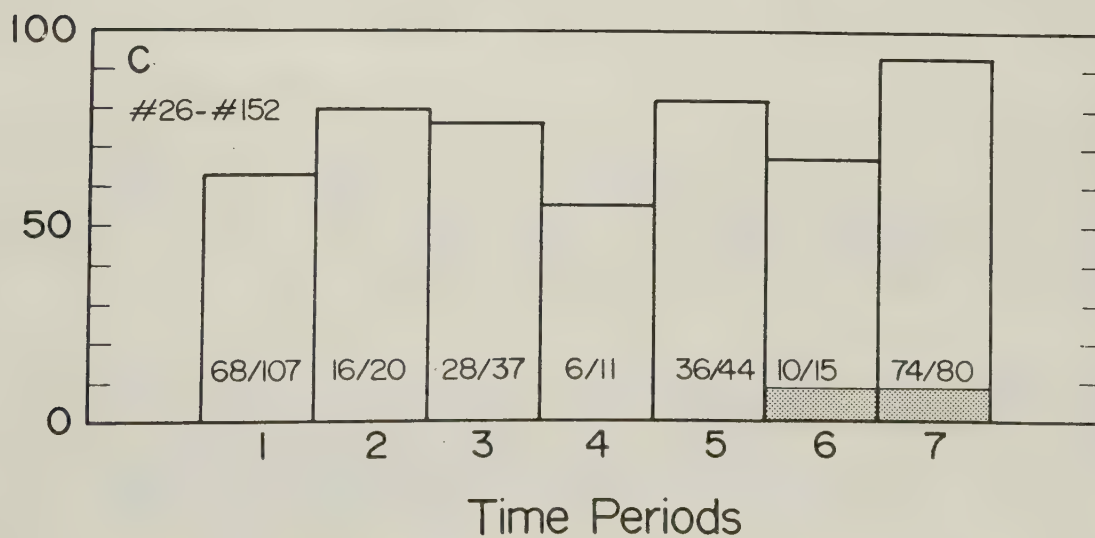
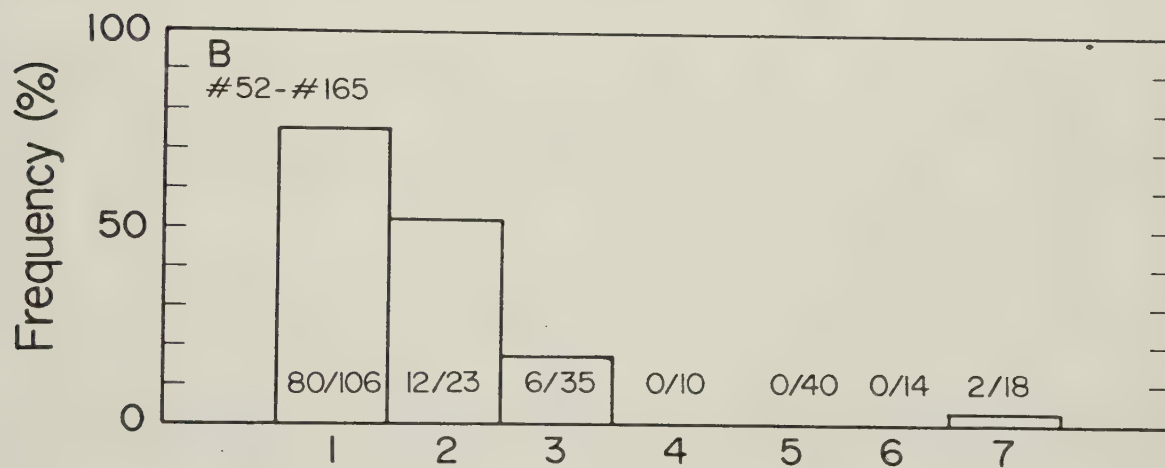
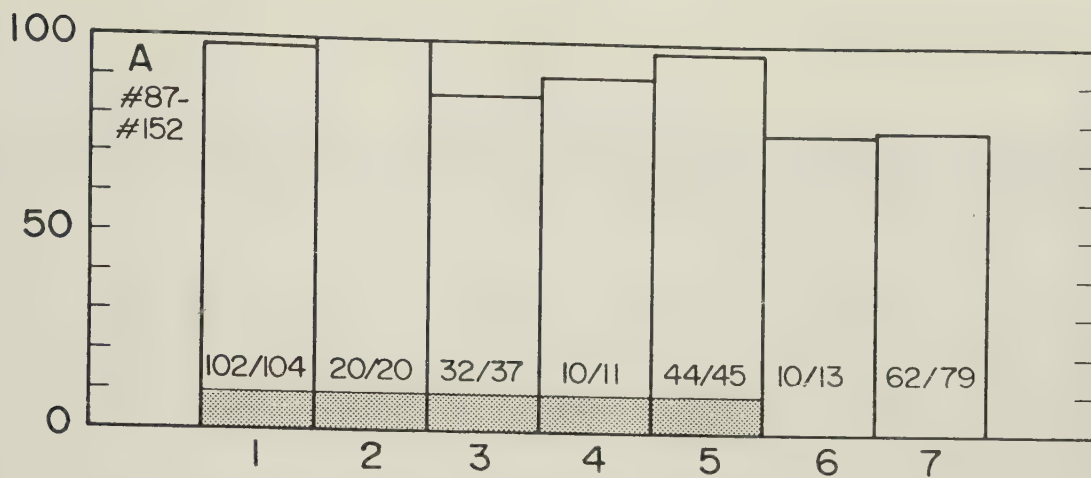


Figure 63. Frequencies of surfacing together for six different comparisons and seven periods shown in Figure 57. Numbers within bars represent number of surfacings within two seconds of each other (numerator) versus total surfacings by those animals in that period (denominator). Shaded areas represent periods when animals were closest together. (Figure continued on next page).



observation. Such runs of surfacings, lasting 24, 7, 12, 5, 18, and 8 minutes ($n = 6$, mean = 12.3 min. $\pm$ s.d. 7.34 min.), and in all cases alternating which animal surfaced first, showed a marked non-randomness of serial order (6 runs, $n_1 = 16$, $n_2 = 15$, $u = 6$, $p < 0.001$).

Dive time means were remarkably consistent for all four animals; #26 mean = 30.5 sec. s.d. $\pm$ 32.41, $n = 150$; #87 mean = 31.8 sec. s.d. $\pm$ 34.03, $n = 144$, #152 mean = 32.0 sec. s.d. $\pm$ 33.96, $n = 144$, and ; #165 mean = 31.7 sec. s.d. $\pm$ 33.35, $n = 142$) with the overall mean of 31.5 sec s.d. $\pm$ 33.42, $n = 580$, and a 95% confidence interval of $\pm$ 2.72 of the mean. The high standard deviation values show that there are large fluctuations above and below the mean, but on the the average each individual dolphin tended to spend an equal amount of time below the surface.

In summary, the four dolphins showed surfacing synchrony corresponding with physical proximity. The fact that all were close together and surfaced together during the initial phase of observations may have to do with disturbance by the boat. Once they became accustomed to our presence a more natural order seemed to be established (Figures 62, 63).

Similar association patterns were recorded for other dolphins from below the surface (Figure 58). These observations were usually much shorter but ranged from 3 to 42 minutes in length. Since the associations were filmed they could then be analyzed frame-by-frame. In a long sequence photographed on April 16, 1980 one could follow the momentary association patterns between three and sometimes four animals. One animal (triangle in the figure) was present through most of the sequence, and associated with two partners (square and diamond), though by far the longest contact was with "square".

"Triangle" split away from partners, each time upon a surfacing. Such partner shifts upon breathing were also features of the other association patterns recorded. One is impressed by the lability of such associations in schools with many animals. It appeared that this tendency to change partners rapidly accelerated with increased activity of the school. Even so there are hints that such encounters are complete events, with solicitations to begin and oscillations at the end.

On occasion we saw hints in frame-by-frame analysis that resistance to the breaking up of a pair came from one partner whose contact, or bout, seemed incomplete; that is, the bout had apparently not run its course and one animal only was ready to seek other companionship. That this seeming asymmetry then led to chase behavior on the part of the dolphins is 'in the eye of the beholder', but one could clearly perceive the asymmetry between the two animals, one giving more evidence of continuing and strong bond than the other. And the tapering off of a bout such as we described in composite, earlier in this section, is a

remarkable exercise in social symmetry as a partner tests the readiness of the other to move on to other partners or activities.

The subtle degree to which one partner responds to the other was seen in our captive group. The adult male, Lioele, had injured himself by spinning out of the tank several years before our observations. He had healed with a bend in his spine and a peculiar wobbly swimming motion. It was interesting and touching to watch Lioele's partners entrain to and imitate this swimming pattern during a bout with him. This imitation allowed us to see that there were solicitations to engage in a bout, as well as what might be called 'acknowledgements' during a later shift of partners.

Lioele tended to spend more time than the others moving slowly at the surface during rest periods. A bout partner of his usually circled him slowly, or floated for short periods and then moved with him. At times a partner passed very close to him, imitating his wobbly swimming motions until he too started to move, and then the two dove and circled together slowly. The converse of this was seen many times at sea when in wild, fast moving bouts a pair dove and twisted in close synchrony, tail beats synchronized so perfectly that only careful film analysis could show a leader or imitator.

During group swimming in the rest period the two captive females sometimes arrayed themselves on either side of Lioele, who swam tilted to one side. In this circumstance the animal on his left usually swam a little higher than he, and the animal on the right a little lower. One implication of this observation is that the pattern markings of spinners are used by spinners as we have suggested, to regulate coordinated swimming patterns.

Aggressive Patterns

One wonders how the seemingly defenseless spinner dolphins protect themselves. It is not that they simply avoid the company of predators such as sharks by use of their superior sensory equipment, since our swimming studies showed them to be accompanied by sharks when offshore, perhaps much of the time (see Leatherwood, et al 1973).

Are jaws and teeth weapons? The delicacy of both the rostrum and the teeth of the spinner dolphins make us doubt this. Both are adjusted to the capture of very small (a few cms) mesopelagic prey and seem much too weak to damage an enemy and are also very subject to breakage.

Nonetheless, spinner dolphins do exhibit behavior that is clearly aggressive. It is used both toward intruders and toward school members. It seems to vary greatly in intensity from mere

negative hints to outright intent to injure. Aggressive behavior seems largely to be relegated to fully adult males, though we reserve judgement because of the difficulty of sexing young males and females of the same size in the field.

(1) Threat Postures

A number of species of odontocetes use an arched or bent posture as an indicator of threat. We have seen variants of such a posture in the genera Tursiops, Orcinus, and, Stenella.

The spinner dolphin uses an S-shaped posture in which the dolphin faces the object of the threat, arches its back, bends its tail upward, and throws its head downward so that from the front the snout is contrasted against the immaculate white of the belly. The pectoral fins are typically spread and may be scissored in rapid slicing motions. The mouth may be opened and closed. This posture may be given by an animal swimming slowly forward or by one that stations in front of the offending subject. Or the animal may swim more rapidly in a circuitous path around, for example, an intruding swimmer. In this case the body curvature is less extreme and the animal rolls from side to side with pectorals slicing, as the tail switches from side to side even as the vertical tail stroke is carried out.

Two observations of such aggressive encounters were noted from the Maka Ala in Kealake'akua Bay. The first took place at 11:00 on March 3, 1980. Four large spinners ran in front of the Maka Ala's bow. Three were thought to be males because of the thickened tail stock and post-anal hump. Sex (male) was determined for one by direct observation of the genital area. The sex of the fourth animal was not determined. Three of the dolphins curved away from the bow in a tight chevron, the middle animal ahead and slightly below the other two. All were within one body diameter of each other. The fourth dolphin approached this group from the side, coming in nearly perpendicular to them, with an exaggerated lateral thrashing of the tail. The dolphin nearest the intruder thrashed a bit in response, still swimming in formation. The intruder may have struck its dorsal fin against the outside animal who then fled, the intruder sliding into its place in the chevron. The aggressor then swam in synchrony with the other two animals.

On July 5, 1980, a topside observer noted a trio of animals, one of which exhibited the S-shaped body posture immediately adjacent to another animal that was swimming belly-up within pectoral touching distance of it. All three then swam down and away from the animal toward which the display was directed.

What may have been a fairly complete aggressive sequence was filmed on June 23, 1980 by one of us (Wells). He swam into a small school (5 animals) traveling along the island coast south

of Kealake'akua Bay. An adult spinner dolphin raced toward him, circling back and forth in front of him. The aggressive posture was assumed by this animal; the arched back, pectoral fins moved forward. As this animal circled, it flexed its body rapidly from side to side, so rapidly in fact that the frames of the film were blurred by the movement at the same time the movement of others in the school were unblurred. At the same time it rolled on its longitudinal axis. An interesting feature of this encounter was the exaggerated sideways movement of the tail, which is also typical of the aggressive swimming of the grey reef shark (Johnson and Nelson 1973). Such sideways movement, while normal for shark locomotion, is at right angles to the tail movement normally used by dolphins, whose tails, of course beat up and down.

Two possible interpretations present themselves. (1) It is possible that dolphins mimic shark aggressive patterns, including tail movement in a plane which they normally do not use. (2) It may also be that such a lateral tail stroke is the most effective weapon for an odontocete, which would bring the thin edge of their flukes against an enemy. Such a use of the cetacean tail is known for both odontocetes (Tursiops; Caldwell and Caldwell 1972) and mysticetes (Eschrichtius; Norris and Prescott 1961).

The S-shaped posture has been observed in detail from time to time in captive spinners, always shown by adult males. On one occasion it was directed at one of us (Brownlee) who was viewing and listening through earphones. This observer directed loud noises (the hard tapping of a metal pencil against the port) at the male as it circled and faced the port. The male then left the school, faced the port, assumed the S-shaped posture with clapping jaws, and then emitted extremely loud double pulsed clicks at the observer. The sound was loud enough to cause ringing of the ears of the listener.

(2) Interpretation

Is there a possible relation to shark aggressive patterns? It is striking how in composite these observations of dolphin aggressive patterns match in detail each aspect of shark aggressive patterns recorded for the grey reef shark, Carcharhinus amblyrhynchos, by Johnson and Nelson (1973). These authors describe shark aggressive patterns as follows:

"The display consists of two locomotor and four postural elements. The locomotor elements include: (1) laterally exaggerated swimming motion and (2) rolling, and later tilting of the body and/or spiral looping (spiral up and down movement through the water, more pronounced in the anterior region). Rolling, although often seen independently of spiral looping, appears indistinguishable from the initial phase of the latter, and both are frequently followed by resumption of laterally exaggerated swimming

(the most common display mode). The postural elements include: (1) lifting the snout, in its most intense form resulting in a distinct bend between the chondrocranium and the spinal column and in a slight opening of the jaws, (2) relatively prolonged and at times marked dropping of the pectoral fins. (3) arching of the back and (4) lateral bending, often more pronounced at the posterior end of the body cavity."

At first glance it is rather simple to mistake a displaying dolphin for a shark. Both are swift and terete. In both, dorsal fins and pectoral fins are not very different. Only the tails and snouts are markedly different between the taxa.

Another parallel is found in the overall body patterns of the dolphin and some sharks, such as the black tipped shark, Carcharhinus melanopterus. Both have dark fins, a dark cape, an intermediate lateral body color and white venter. Both are about the same size as adults and have widely overlapping geographic ranges. Both are common in the passes of tropical atolls.

The relation of the shark tail and the post-anal hump of some tropical male dolphins is of interest. The hump is a marked rounded swelling of the ventral caudal keel just posterior to the dolphins's anus. It reaches large size in the eastern tropical Pacific spinner dolphins (see Perrin 1972), and in the roughtooth dolphin, Steno bredanensis (Norris 1967). The hump is composed of connective tissue. It is modestly developed in the adult male Hawaiian spinners and allows them to be sexed from a distance (Figure 64).

We view this hump as a structure that enhances a sign. In aggressive posturing the dolphin's tail stock is bent downward and forward. This thrusts the vent and genital area forward. In this same posture the male shark exhibits a similar "swelling" because his tail, posterior to the vent, carries heavy claspers and the anal fin (Figure 65). The match between the post anal hump and paired claspers is sometimes even more precise, since very well developed humps may be folded anteriorly.

This relationship between the appearance of sharks and dolphins may be carried one step further. Adult male spinner dolphins develop increasingly erect and tall dorsal fins as they age. This is especially marked in the eastern tropical Pacific spinner, in which in old males the dorsal fin may be very tall and give the appearance of "being put on backwards"- that is its anterior margin may cant slightly forward from the vertical. Might it not be that during aggressive posturing as the body is arched the fin is emphasized in both male sharks and dolphins?

It seems probable that the dolphin mimics the shark. Every feature of the territorial behavior of the shark is contained in

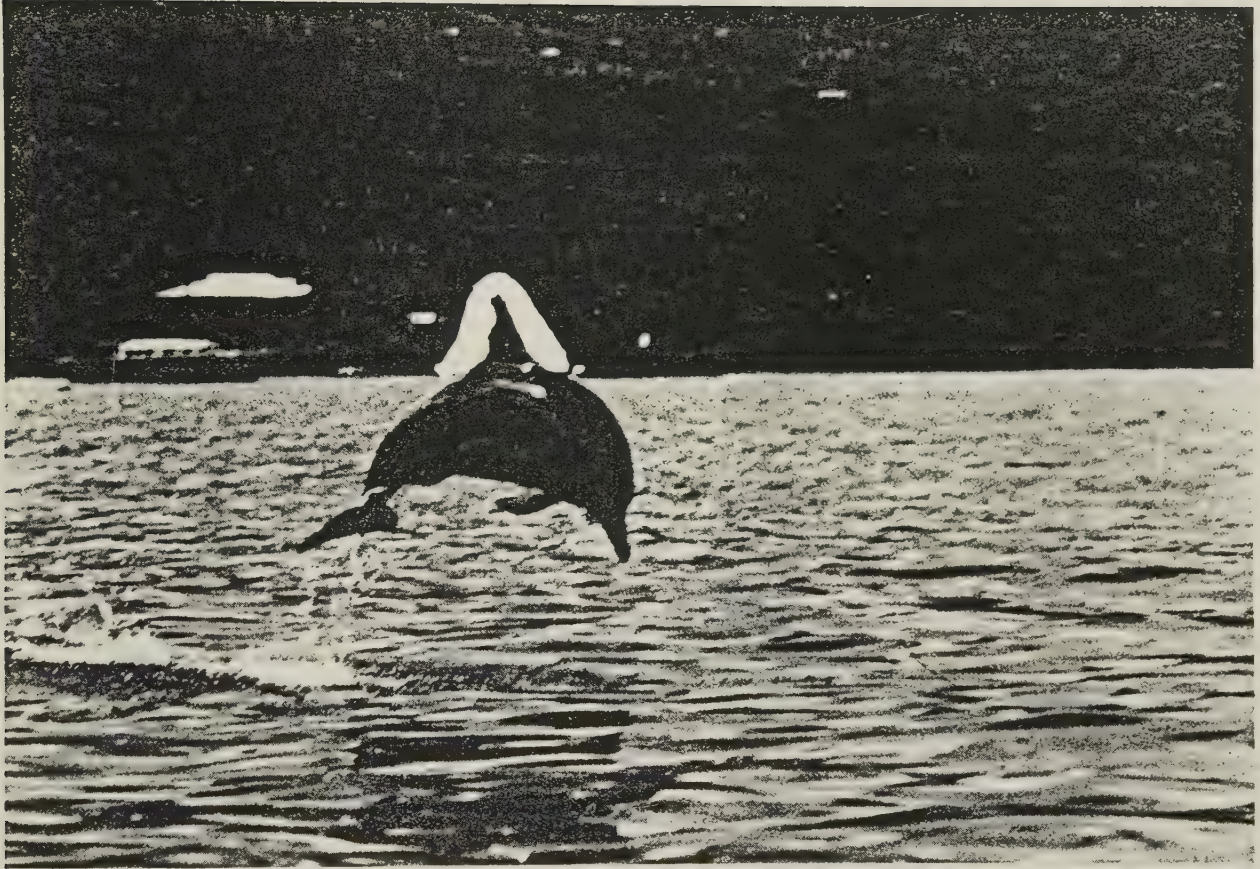


Figure 64. "Finger Dorsal" (Dolphin #1) leaping. Note the postanal hump that marks him as an adult male. Photo retouched to highlight dorsal fin.

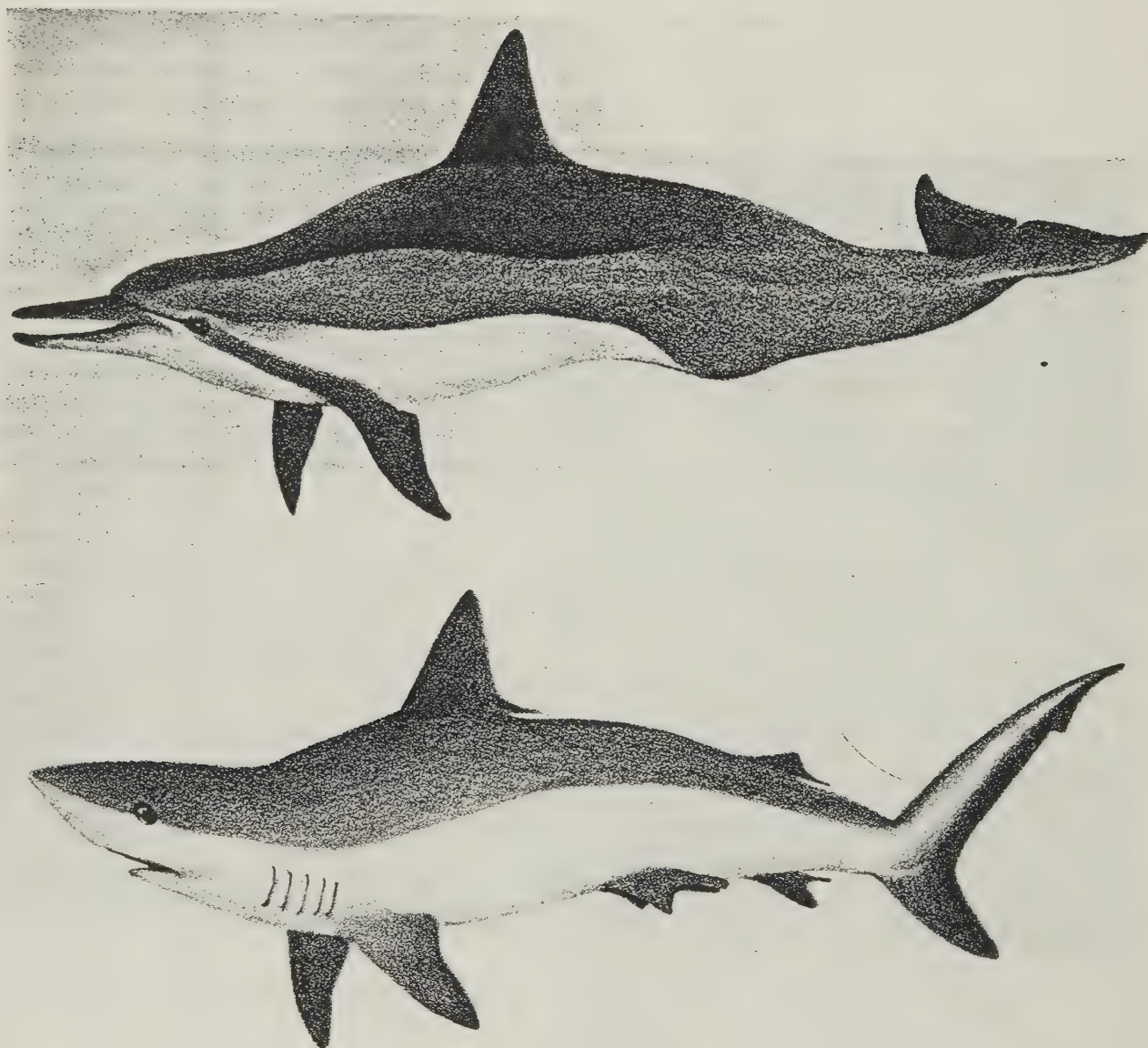


Figure 65. Aggressive postures in male spinner dolphins and the Gray Reef Shark. See text.

the dolphin patterns, including the lateral movements of the tail, which in the shark are basically locomotory, but are in the wrong plane for the dolphin. The exaggerated swimming of the shark, the posturing, the opening and closing of the mouth, and the scissoring of the pectorals are all there.

How might this possible case of dolphins mimicking sharks be used? Clearly enough the patterns are used within spinner schools as we have described above. It also seems likely, judging from widespread evidence of shark attack on dolphins (see Predation) that sharks are important dolphin predators. The behavior pattern may be used outside the dolphin school directed toward these predators. This presumes that the aggressive patterns of sharks are effective within their own species, and not just to territorial intruders of other species.

Do dolphins actively defend themselves against sharks or do they simply avoid them? If the proposed mimicry is to be effective against sharks it has to be shown that the inoffensive dolphin actually uses it against them. One remarkable observation, that of Stewart Springer, a shark biologist (AIBS 1967), is, to a degree, instructive. Springer, working in the Gulf of Mexico on a 250 ton fishing vessel, watched a school of approximately 50 common dolphins (a species closely related to the spinner dolphin) approach the side of the ship. The dolphins arrayed themselves along the ship's rail, with their young closest to the vessel. Springer noted the dim shapes of sharks 30 m away in a perimeter toward which the outer dolphins periodically rushed. The sharks retreated from these rushes, though injuries to the tails and fins of some dolphins were noted. The observations continued for about an hour until a heavy rain squall enveloped the vessel. When the squall had passed both sharks and dolphins were gone.

How the sharks were repelled is not clear, but there was segregation within the dolphin school and the adult dolphins somehow served as a protective shield. No direct evidence of mimicry is involved.

It is clear that loud sounds are sometimes involved in aggressive patterns, but whether or not they are integral to the effectiveness of this proposed mimicry is unclear.

(3) Open Mouth Contact

Dolphins not infrequently nip at each other. We have seen open mouth contact including raking with the flat of the jaw in active schools during high levels of social interaction, including group caressing.

A fairly typical example was recorded on August 31, 1980, from the Maka Ala, in Keakake'akua Bay. At 10:10 an active

subgroup of about 12 dolphins, mostly pairs of adults but including one calf, was encountered. One threesome was observed in active interaction. One of the animals opened its mouth and pressed the side of its tooth row against the back of another animal, behind the dorsal fin, and then quickly touched the same area with its pectoral fin tip. The same pattern was repeated again but this time against the area of external auditory meatus. This led to a chase by the recipient, and another pressing event, this time with jaws closed.

Later (10:18) in the same school amidst an extremely intense outburst of noises including loud whistles and buzzes, a caressing subgroup of about 12 tightly interweaving dolphins was noted. In this group, belly tilts were frequent and open mouth contact was noted. There was literally no space between participants.

Open mouth contact is sometimes associated with chases. On September 1, 1980, in Kealake'akua Bay, a subgroup of about five dolphins was seen traveling at the front of an active school. One dolphin pressed its open mouth against the uppermost dolphin of a belly-to-belly pair. The pressing dolphin then swung under the upper animal in the inverted position. At this point another dolphin nipped at the flukes of still another schoolmate. This precipitated a rapid nearly vertical dive by the nipped animal, fleeing from the the aggressive animal and one other. At one point in this chase both pursuing animals swam belly-up and disappeared. Directly afterward a cacophony of sounds was heard and the viewing vessel passed through a bubble field 3 m across extending downward as far as one could see.

Scars that apparently come from open mouth contact are frequently seen on dolphins of many species. Since the teeth of dolphins tend to splay out from the jaw, such a raking motion of the jaw can furrow the skin even though no serious wound results. The scars consist of groups of parallel scratches, obviously from conspecifics since the gap between scars matches the usual gap between the teeth of the species.

Mating

Sexual activity in nature peaks during summer and fall. this was mirrored in high levels of reproductive hormones and sexual behavior in captivity during this same period (Wells 1984). Then it was not uncommon to see intromission in caressing groups. Our field records show 16 examples of mating between June 26 and October 14, 1980. In these cases the observer saw either the penis, or noted belly-to-belly contact with thrusting.

The matings seemed to be promiscuous, with more than one male achieving intromission with a single female during even very short observation sessions. For example, on August 31, 1980 two males were observed mating with a single female. During this

sequence the first male righted himself after intromission and remained close to the left side of the female. A second male turned belly-up above the female and then rubbed against her right side as he rolled down into mating position under her. As soon as the second male's penis became visible, just before intromission, the first male darted off to a nearby adult (unsexed) did a belly-up to it, and then chased it while it tried to swim away. A receptive dolphin was rarely alone for long.

Birth, Nurture and Juvenile Groups

We saw neither births nor identifiable newborn animals at sea in this study. It may be that we simply could not discriminate newborn animals from those a few days old. Very young calves were frequently seen in the company of other calves, subadults, or adults. The accompaniment of such very small dolphins by other young animals, swimming separated from evident parents, was striking to us. It indicated that very early in the life of a spinner dolphin, months before weaning, sorties away from the mother with other calves is normal behavior. Fairly frequently groups of up to about six calves were seen swimming together within a larger school.

(1) Calf Behavior

Dolphin calves are often among the most active energetic members of a school. Routinely, we observed young spinners, especially the larger ones, darting away from their companions and then rushing back to them, the sorties covering 20 - 40 m. A calf might pump its tail about twice as fast as an accompanying adult in rapid swimming. Or it might engage in assisted locomotion in which it takes a position alongside as adult, usually with pectoral fin contact, and is carried along by the water flowfield sweeping past and between adult and young (Norris and Prescott 1961).

The movements of calves tend to be "exaggerated" with much wiggling, tilting and rapid course changes. We identified the "nursery areas" of schools, which are open volumes of water within the school ringed by adult animals (Bateson 1974, called them "playpens"). Calves sometimes were seen chasing one-another, rolling over, touching bodies, fins and genitals in apparent high-speed parodies of adult courtship and caressing.

Calves occasionally rode the bows of our vessels, most commonly in the company of an adult. Occasionally, calves appeared to be inquisitive, and more often than the adults, approached the boat head-on, or turned and tilted to look in the window of the Maka Ala.

Calves are remarkably aerial. Frequently one or two were seen leaping and splashing at the surface while the majority of the school rested quietly. At times such activity lasted more than an hour, and such calves practiced aerial patterns that defied our system of categorization. This suggests that practice is important in establishing the adult aerial repertoire. On the other hand calves were sometimes seen performing well-coordinated spins.

An attending adult occasionally jumped with a young animal although it more often lingered near by. During active periods for the school simultaneous leaps by an adult and young were sometimes seen. Sometimes adult and young pairs were seen swimming in synchrony and breaking the surface in a simultaneous leap. On one occasion three adults and a young dolphin performed 13 simultaneous arcing leaps in a row.

A particularly well marked mother-young pair, dubbed "Temple Baby" and "Mottled Mom" spent much time near our boat and tended to stay somewhat apart from the rest of the school. To give reader a glimpse of mother-young relations within a school we have condensed our observations of this and other pairs.

On one occasion, they performed a series of three tandem arcing leaps during the morning activity period. Later in the afternoon these two were seen spinning simultaneously and then in one spectacular display they performed a high arcing tandem leap in opposite directions, passing each other within a few cm at the apex of the leap. During this leap "Mottled Mama" belly-tilted toward the calf.

On a few occasions, when a resting school was engaged in an extended dive (ca. 3 min.) an adult-young pair rose out of the carpet formation that moved slowly along the bottom. Sometimes the adult leveled off about midway to the surface while the calf darted up, took a breath, and then rejoined the waiting adult. Later, the entire school surfaced and the pair reentered it.

Sixteen belly-ups by young animals were recorded. For the most part these did not seem to be reunion gestures but occurred within tight pairs. Most were performed by calves swimming below the mammaries of adult females and often involved contact. Only one involved a juvenile and calf.

One of the belly-to-belly incidents mentioned above was indeed a situation of reunion, involving "Mottled Mamma" and "Temple Baby" (Temple, a female, was by this time a juvenile) (August 15, 1980). The pair was seen together in the morning. The juvenile darted about, sometimes spinning alone. At 09:47 "Mottled Mamma" was alone in a tight swirling group of six adults, in which much body tilting and contact was taking place. The next sighting, at 09:49, involved "Temple Baby" belly-up below her mother, with her rostrum touching the adult's

genital/mammary area.

A tight subgroup of adults in which dorsum-up beak-genital propulsion was observed swam near by. A little later, at 10:05, the pair was seen again, side by side, trailing a swirling mass of adults in group caressing. Twice during that morning, at 09:22 and 10:10, subgroups of three juveniles were seen doing belly-ups and belly-tilts toward each other. Their rapid interweaving prevented the observer from determining if "Temple Baby" was amongst them.

Calves or juveniles were frequently seen in groups involving belly-tilts, belly-ups and intromission between adults. Six of the 16 belly-ups performed by young animals occurred in groups in which belly-up adults, but not the mother, were also seen.

In the 10 cases in which presumed mothers were seen belly-up or tilted toward another adult, the nearby young were always dorsum up. In fact, in all such triads the inverted animal was invariably the "mother". The young occasionally made contact with its inverted mother but was never seen touching an escort.

Subadult behavior was in many respects like that of the younger animals. Subadults were typically highly energetic, were often paired with adults, and were seen performing assisted locomotion with an adult.

A distinguishing feature was their independence, which was greater than that of calves. They were more apt to change swimming companions and to put a considerable distance between themselves and others than were calves. They were seen paired with large males and females. Rostrum-to-genital contact, a common pattern with calves, is rare in subadults.

Young animals, when swimming with an adult, usually maintained a position somewhat above or below the midline. In part this probably relates to the hydrodynamic advantage it confers (see Norris and Prescott 1961), but it also may have social meaning. Small calves frequently swam below their adult consort, often with their heads aligned with the adult's genital area. Since calves in this position swam actively, the position probably relates to protection and nutrition rather than hydrodynamic advantage.

In 45 observations of a calf being accompanied by two adults the calf usually (40 cases) associated clearly with one adult. In the other five cases the calf swam between the two adults, and during our observations was not clearly associated with one or the other.

Most of the time when adult-calf pairs were more or less centrally placed within the school envelope the school was engaged in evasive maneuvers, trying to avoid our vessel or

others in the bay. These pairs were often completely surrounded vertically and horizontally by adult animals, a disposition reminiscent of the "teacup formation" described by Norris, Stuntz and Rogers (1977) for dolphins trapped within tuna seines. In undisturbed schools adult-calf pairs were to be found anywhere within the school envelope, often at the periphery.

The Question of School Leadership

How do spinner dolphin schools make decisions about where and when to move? How, for example, is a nighttime feeding school directed to swim toward shore and then to enter specific coves to rest? Three choices seemed possible. First, there might be a single leader. Second, there might be a leadership class (say, adults) that gives directions, and third, there might be a collective memory by all animals. It seems evident to us that dolphin schools always possess the requisites of a reaction system, or what we call a sensory integration system. Superimposed on this basic communication matrix in alert undisturbed schools is, we believe, a system of group leadership.

If dolphins were following a single leader, then the loss of that leader should leave the school bereft. There is no evidence of this. The extreme fluidity of schools seems a clear indication that schools can be formed, to a very considerable degree at least, of available individuals, and yet these schools carry on daily activity patterns. The requisites of leadership must therefore be widespread. We can say that we never saw juveniles or calves alone though such groups are frequent within the school envelope.

The smallest schools we saw apparently all contained adult males. It was in them that some of our best observations of aggressive patterns were made. Our observations of turning maneuvers suggest that adults, probably of both sexes, initiate this function in undisturbed schools. So, it seems that adults of both sexes are the group decision makers.

Underlying all such patterns are the basic communications features of the school; its sensory integration system. This system operates in immediate fashion to direct stimuli, but it is blind to geographic or other goals that might be found in the collective memories or motivation of the adult members of the school.

Locomotion

When a spinner dolphin glides, its tail trails behind at the level of the ventral surface of its belly rather than at midbody as one, a priori, might expect. It is from this rest position that the tail oscillates in the up-and-down stroke. The top of

the stroke is reached when the flukes rise to about the highest level of the back. The bottom of the stroke extends downward an equal distance below the resting point, or to about the tips of the extended pectoral fins (Figure 66). Frame-by-frame analysis indicates an equal time in the up and down strokes, though the method is not precise due to the speed of fluke movement and the relatively modest frame rate (15 f/sec.) of our camera.

The effect of the upper limit of fluke excursion is to keep the flukes in the water even on powerful upstrokes. The dorsal fin tip may mark contact with the surface for the animal and even when the animal surfaces to breathe the flukes will remain below the surface. It may also allow the animal to gauge the position of its flukes when approaching others in its school. On the down stroke the pectoral fin tips may indicate for the animal where the flukes will be, even in close locomotory patterns such as group caressing.

It is hydrodynamically crucial that the dolphin's upstroke end well below the water surface because the power of that stroke is substantially lost unless the flukes are loaded with an overburdening column of water (Lang 1966). In fact, one can 'see' such power loss because both dolphins and whales leave 'foot-prints', which are an upwelling of water from the upstroke. But the losses are minimized by the depth of the top of the upstroke. Rapidly swimming animals traveling at the surface may avoid the problem by turning on their sides. This was noted in speed trials of a dolphin required to traverse a shallow race course (2-2.5 m depth) (Lang and Norris 1966).

Respiration

Our underwater films gave us an unusual opportunity to describe in detail the timing of respiration. As far as we know this provides a unique description of this process for odontocetes. It goes quite a way toward explaining how dolphins can extract relatively water-free air when they breathe at the often turbulent sea surface. One can imagine the problem by envisioning the difficulty a dolphin might have obtaining breathable air during a storm at sea, when the air-sea interface becomes an indistinct boundary.

Our films reveal the following process: A surfacing dolphin bends its anterior body upward from the horizontal swimming trajectory. It does so at an angle that brings its snout tip and dorsal fin tip to the surface simultaneously, or nearly so. As the snout tip touches, and while the blow hole is still 2-3 cm below the surface, expiration usually begins. In our films one often sees this first as the extrusion of a silvery bleb of air over the blowhole. This bleb is often directed anteriorly over the surface of the head. At this point the blowhole opening is a crescentic slit. The slightly open blowhole valve causes air to

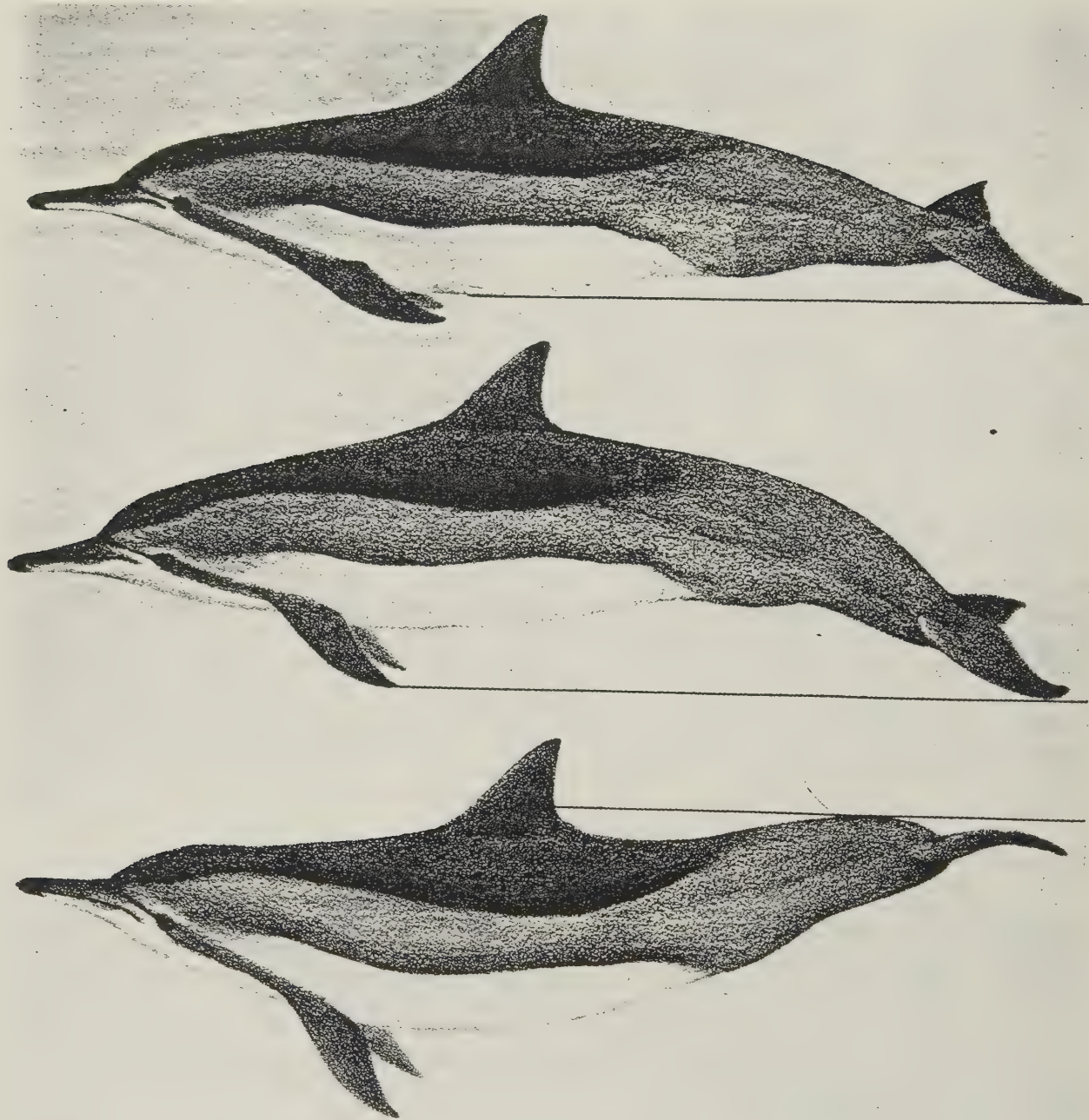


Figure 66. Fluke excursions of spinner dolphins. (Top) In glide flukes are at level of lower belly (Center) At bottom of stroke they do not go below tips of pectorals (Bottom) At top of stroke they rise to midway between back and tip of dorsal fin.

move forward under the hard posterior lip of the blowhole essentially in the plane of the animal's body (Figure 67). Sometimes this initial expulsion of air occurs well before the animal reaches the surface and a flattened bubble of air may then move backward across the animal's head as it swims forward (Hubbs 1965, Figures 67,68).

But, the usual occurrence is for the bleb of air to appear and for the surfacing animal to swim into its own exhalate. As we know from the work of Kooyman and Cornell (1981) the velocity of such exhalate in air can be very great - as much as 1681 m per second.

This high velocity blast of air imparts momentum to the water around the bubble just as the dolphin breaks the surface. This creates a spray of water droplets blown outward at quite high velocity, scouring the air above the rising animal's blowhole. At first this plume of fast moving droplets is directed forward into the line of the dolphin's ascent, because the blowhole is still incompletely opened and air is deflected forward by the rigid posterior blowhole lip and the partly open blowhole valve. As the animal ascends, the blowhole opens more widely and the air rushes more and more vertically above the animal's head. The animal begins inspiration in this highly transient space of scoured air. The roll of the dolphin now begins to take it below the surface again.

The dolphin hits the surface of the water with its anterior head, creating a hollow of air in the surface of the sea as it descends. Inspiration is completed inside this highly transitory space. The Dall's Porpoise (Phocoenoides dalli) creates the most obvious of such breathing spaces in the water surface, but these are also present during spinner dolphin breathing sequences.

We have timed a series of respiration events from our film analysis (Figure 68). The total respiratory durations are smaller than those reported from beached captives, where total durations for Tursiops typically took 0.7 - 1.0 seconds to complete (Kooyman and Cornell 1981). Spinner dolphins not infrequently breathe in and out in as little as 0.5 - 0.6 seconds.

One can sometimes see the exhalation blast from above the surface. It looks a bit like water spraying from a lawn sprinkler, followed by a more vertical "spout". The vertical blast may reach a meter in height. The upper portion appears to be condensation and was usually best seen when resting schools traveled close against the dark Kealake'akua Bay cliff in the cool air of the morning.

The Possibility of Prey Debilitation

Bel'kovich and Yablokov (1963) calculated that dolphin clicks contain very large energies because they were extremely

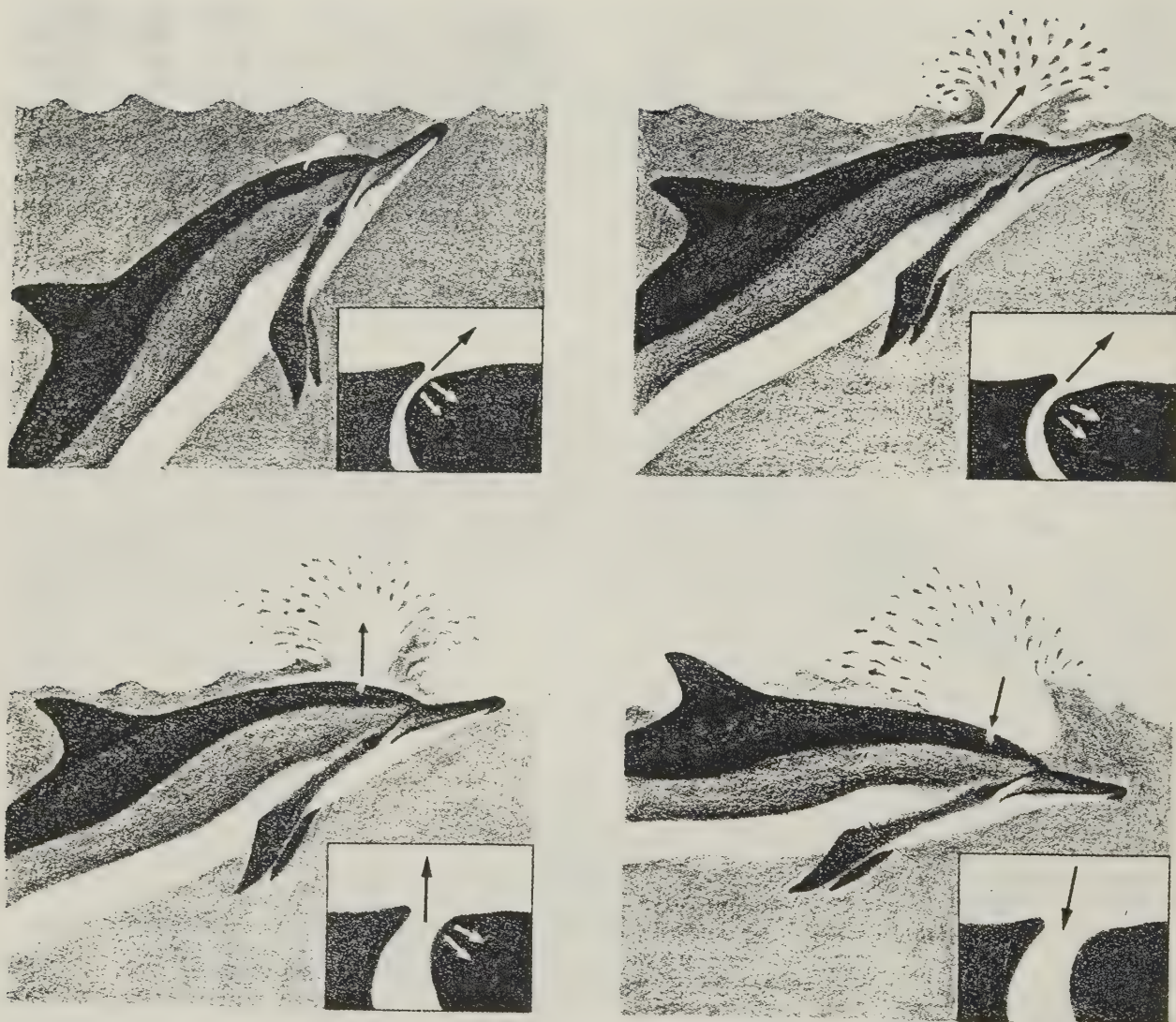


Figure 67. The respiratory cycle of a surfacing spinner dolphin, as determined from frame-by-frame analysis of moving picture films. (A) Jaw tip touches surface and bleb of air appears over blowhole, directed forward. The dolphin swims into it (B) Water is forced forward into path of swimming animal scouring air above rising animal (C) With blowhole more widely open blast is directed upward above exposed blowhole (D) Snout thrust downward excavating hollow in surface water inside which dolphin completes inhalating. Cross-sections of blowhole show conformation expected at each stage. Note that during inhalation blowhole is wider open than during full exhalation.

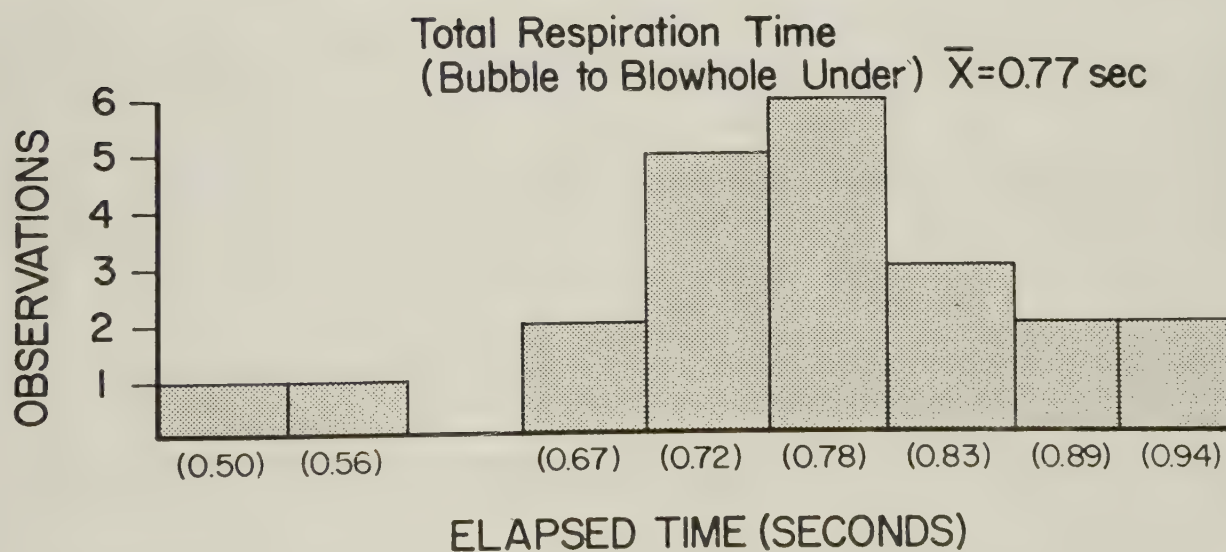
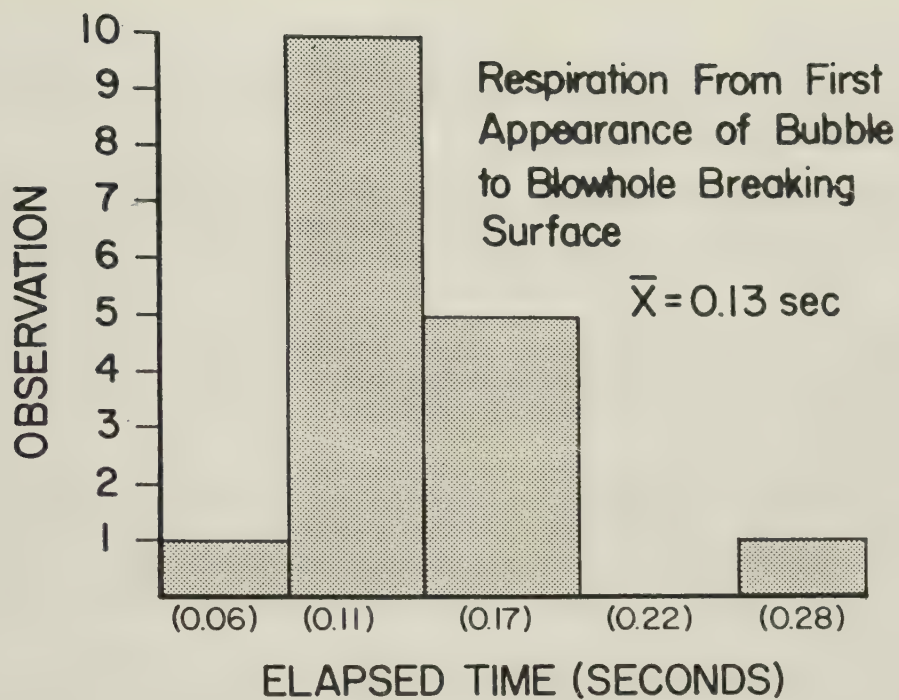


Figure 68. Respiratory sequences timed from frame-by-frame analysis of moving pictures.

brief, intense, and contain high frequencies. They suggested that such sounds might stun prey. Even small dolphins (some of which use very high frequency sound) might produce clicks of as much as 6.5 atmospheres pressure.

Pressure differentials in water are indeed capable of producing tissue damage, as is known from the effects of underwater explosions. These relationships were recently reviewed by Norris and Møhl (1983). In this work the authors relate the possible origins of prey debilitation to the development of narrow echolocation beams, which while increasing the range of the animal's system also concentrate their energy and account for the very intense sounds modern odontocetes use.

These authors suggest the generation of narrow beams is related to the development of the broad odontocete head (at the level of the sound generators). The reduction in snout length and the loss or reduction of teeth suffered by many modern odontocetes may, the authors feel, be related to possible sonic prey debilitation.

It was with many of these ideas in the background that we tested the feeding behavior of spinner dolphins using a small school of live fish. The dolphins we used were the Sea Life Park captive school. They were routinely fed fresh frozen fish and no one knew what their reactions might be to live fish.

We obtained a school of 24 akule (Trachuropsis crumenophthalmus) from local fishermen and transported them to the dolphin tank. The school was divided into two; one half placed in the main fish exhibit of the oceanarium, and the other half introduced into the 27 m diameter pool occupied by the dolphins. The fish were approximately 20 cm in length, or about 2-3X the length of usual spinner dolphin prey in nature (see Food Item Summary).

The control group in the main fish exhibit was quickly harassed by a school of large jacks (Caranx sp.), from whom they sought protection by swimming among the tank rockwork. By the time of test completion some of the akule were raked by the teeth of the jacks and some may have been eaten.

The other fish, which were introduced into the dolphin pool, were observed from the viewing room (see Materials and Methods, and Figure 6).

The fish quickly formed a tight school at the deepest part of the tank and within a few seconds the two female spinner dolphins began to make runs at the fish, each time emitting a whining click train. These runs were quite stereotyped, both with regard to the behavior of the fish and the dolphins. The dolphins circled the fish from above and then rushed at the fish school toward its side (see Figure 69), emitting high repetition rate click trains concurrent with rapid head scanning directed at

the fleeing fish.

Click emission appeared to begin about 2 - 3 m from the nearest fish and to cease as the dolphin passed the school. The fish school split upon the approach of the dolphin, each part circling tightly toward the passing dolphin's tail. This had the effect of restricting the time during which any of the fish were actually ensonified by a dolphin to no more than from 1 - 3 seconds on any pass.

For the first hour, involving about 12 runs, no effect of ensonification could be noted upon the fish. The observers left for about one hour and when they returned, circumstances were dramatically different. By this time the fish school had begun to depolarize, some fish wandering away from the school in long vagrant traverses. The school also proved nearly incapable of swimming through a modest vortex at the tank drain, a feat that would have given them no trouble upon their introduction into the tank.

The dolphin's behavior had also changed. The two females had begun to chase the vagrant fish, holding them within 1 cm or so of their snout tips while clicking across the fleeing fish with extremely tight and rapid head scans.

One of the fish that seemed least able to school with its schoolmates was repeatedly ensonified and finally changed color from silvery to lemon yellow, and it was ultimately caught in the drain vortex and sucked down from about 2 m above the tank bottom and out of the tank.

The dolphins made no attempts to eat these fish, even though they clearly could have done so at will. In retrospect this seems understandable because the fish were so much larger than any they normally ate, either in captivity or nature, and because the dolphins had long been on a diet of small frozen fish presented at certain hours of the day.

What seemed remarkable was the quite stereotyped behavior of the dolphins in dealing with these fish. The approach to the side of the school, the whining click trains and the short rapid head scans were each reminiscent of the click train bouts we described earlier (see Click Train Bouts).

The placement of the fleeing fish very near the snout tip (about 1 cm) suggests that these dolphins had placed the fish in the near field, a region of very high and rapidly changing intensity in the emitted beam. The rapid head scans could produce abrupt changes in intensity at the fish, and the close proximity could subject the fish to both displacement (near field) effects and pressure (far-field) effects. It is also interesting that the snout tip is an emission site separate from the melon above (see Norris 1968, Diercks et al 1971).

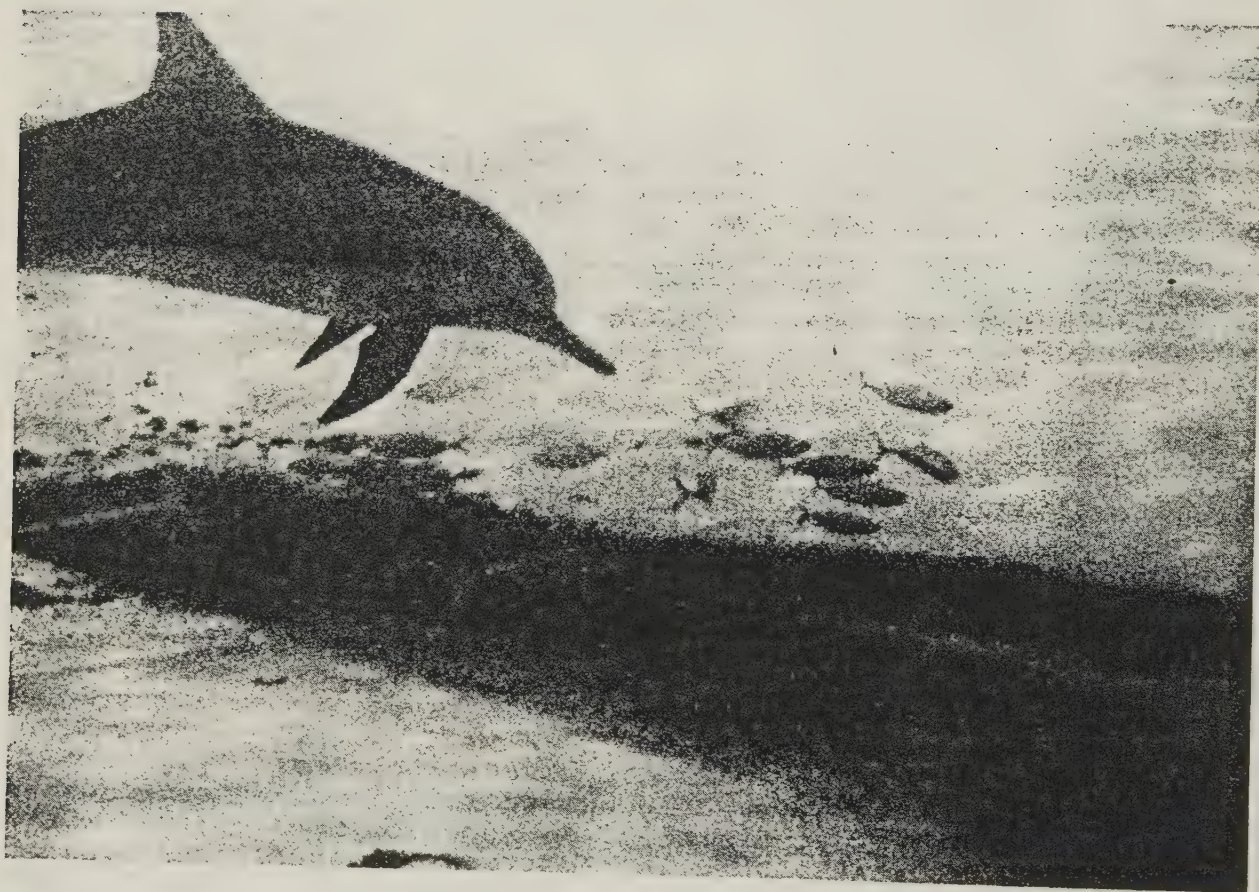


Figure 69. A female spinner dolphin ensonifying a school of akule, Trachuropsis crumenophthalmus. Note extreme swelling of the dolphin's forehead. Sea Life Park oceanarium.

Can we be sure that the effects noted on the fish were produced by the sounds of the dolphins? Clearly we cannot, and further experiments are needed. First, the debility of the fish could have been due to lactic acid debt built up by the fairly consistent harrassment by the dolphins. This seems unlikely though, because control fish, even though pursued by jacks, continued to school normally. Likewise we can rule out effects of handling. If present they should have appeared in both groups of fish.

The debility of the fish appeared to involve equilibrium, and the sensory system that allow fish to school (head canals and lateral line system).

At any rate the observations are interesting ones that deserve further investigation.

Swimming with Spinner Dolphins

The swimmer's camp was situated at Makalawena Beach, adjacent to one of a series of small coves typically frequented by the largest resting schools on the Kona coast.

Our free-swimming studies, while primarily an attempt to test the method, provided important data and insights. Most observations were similar to ones obtained by other means. New insights concerned the reactions of dolphins to different rest coves, observations of the association of sharks and dolphin schools, aggressive behavior, play, and since the observation site was distant from Kealake'akua Bay, important data on differential school composition and individual movements along the Kona Coast. The following are excerpts from notes taken by swimmer-observer Jody Solow, while other data are introduced under their proper headings elsewhere in the text.

"Our method, once dolphins had settled in the bay off our base camp at Makalawena, consisted first of waiting for these animals to approach the boat and to begin to pass it slowly. This I took to be a signal to go swimming. I put on my wet suit jacket, mask, fins, snorkel, picked up my diver's flag and Nikonos III 35mm camera and slipped into the water. I immediately began to utter vocalizations (a facsimile of a dolphin cry) to 'announce my presence'. The rationale for this is that a person approaching silently might be taken as an enemy, in the same way a shark would be, while a phonating foreigner might be regarded as more friendly. Of course their acute hearing made them aware of my entry into the water.

While continuing to emit sound I swam toward to dolphins, and then hung at the water surface vocalizing less frequently and waiting for the dolphins to swim near me, which they usually did.

When two or more schools were involved, which was frequently the case in this area, there was often a great difference between the groups with respect to aerial activity, vocalization and underwater behavior. This seems related to the degree to which each group had entered or aroused from the rest period. One school might be closely packed, more synchronous and slow in its movement, less vocal, less aerial and less active underwater than another nearby school.

From active schools I sometimes heard mimics of my vocalization. The more active the dolphins were the more vocal they were. I heard chorusing whistles, various burst pulsed signals and click trains. Some burst-pulsed signals were very distinct sounds. One sounded like the twanging of the banjo, another like the laugh of a chimpanzee, and another like the rubbing of a finger across a balloon. The wealth of communications possibilities in such burst-pulsed signals seems very great, and seems little appreciated.

I could usually hear where the dolphins were before I could see them. It seemed that the dolphins stayed between the boat and the shore and/or me much more frequently (85 - 90% of the time) than they passed offshore of me. I wondered if this is a reaction of dolphins to danger.

A frequent school shape was a rough oval. During the day such oval schools moved throughout the bays, often as close as 5 m to shore. Such oval schools are relatively inactive and little interaction was noted among their members, but they usually did not swim in complete synchrony. Some whistles were heard in such schools.

I was sometimes allowed to come very close; within 2 m or less at the Makalawena area, and even closer off Lanai Island, where I actually played with a dolphin. This was "Linus", possibly a male, who played "catch" with himself by carrying on his pectoral fin a piece of flotsam (a piece of black polyethylene sheeting blown into the sea from the nearby pineapple fields), then letting it go and returning to pick it up with his flukes or rostrum. While I watched he played this 'game' for some time. Sometimes he let it go in front of me. The first time he did this I dove down to retrieve it, but just as I was about to grasp the polyethylene he darted rapidly in and took it away on one of his pectoral fins (Figure 70).

Later in the day he released it in front of me again and I succeeded in grasping it. I swam with it for a while as he swam back the forth about 2 m in front of me emitting a loud fast click train. I let go of the 'toy' and he immediately took it on his pectoral fin and swam away. Later that afternoon the sequence was repeated.

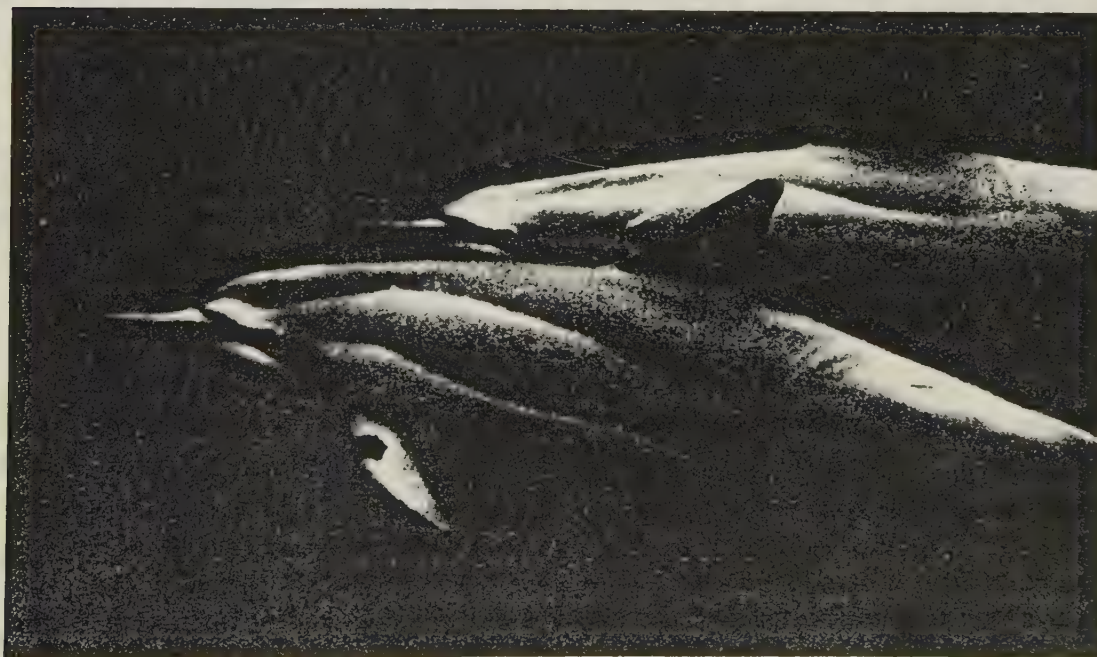
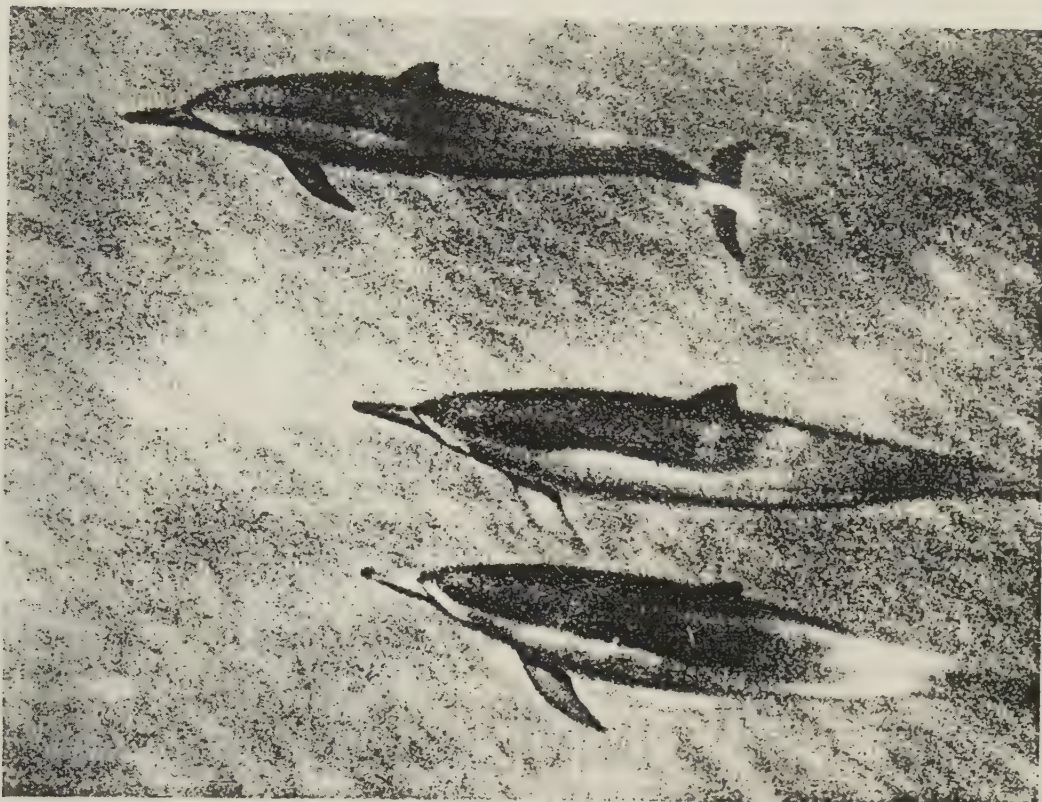


Figure 70. Spinner dolphins carrying objects, off Lanai Island. Photographs by Jody Solow.

On another afternoon "Linus" and another dolphin that frequently traveled with him (it had a pronounced white scar just below its dorsal fin) were playing 'catch' with pieces of plastic. Linus carried a garbage bag and his consort carried a small clear plastic bag. On another occasion this pair was seen passing a piece of plastic from one to the other.

As the dolphins descended into rest they became somewhat less approachable and we usually left them alone to avoid harassing them.

I noticed that the dolphins typically swam quickly around points of land such as those at Mahaiula and Puukala and then slowed down considerably after rounding them. Do such points mean danger because deep water is nearby? Certainly the closer the dolphins swim to shore the quieter they are apt to be.

Only once did I observe aggressive behavior, and that was off the Island of Lanai. A trio swam together. One animal positioned itself belly-to-belly with a second animal, and the third tried to take up position between them. The first animal darted over to the third and displayed with such evident aggression that I was frightened and left the water. The two dolphins confronting each other moved with short, quick movements and contorted their bodies into the S configuration with heads down and to one side, with mouths open, exposing their teeth. They shook their heads and swished their tails sideways. I don't recall if any sounds were emitted.

Sharks were occasionally seen swimming quietly adjacent to the dolphin schools. They were most frequently seen while swimming with the dolphins schools off Lanai Island. On one occasion there I noted the dolphins' school in obvious agitation and as they passed saw the gray shape of a medium-sized shark cruising at the same speed as the dolphin school. I left the water."

Food

Previous data on spinner dolphin prey from four sources indicate that the species feeds on small fish, cephalopods and shrimp at night in relatively deep waters, diving at least to 200-300 m (Fitch and Brownell 1968, Perrin et al 1973, Norris and Dohl 1980). These characteristics of feeding are further supported by the analysis of stomach contents from a single spinner dolphin captured for tagging in this study. This dolphin was captured at 13:30 on 22 April 1980, and died within minutes. The entire animal was sent fresh to the National Marine Fisheries Service, Southwest Fisheries Center for tissue analysis. No fleshy material was collected from the stomach but fish otoliths, scales, eyes and squid beaks were found and preserved in 70% ethanol. The otoliths were identified by John Fitch. The squid beaks were not identified.

Table 7. Summary of food items known from *Stenella longirostris*. For fish, the total number of otoliths collected, the percentage of the total that is comprised by each taxon, the number of dolphins in which each kind of otolith was found, and the percentage of the total number of dolphins examined in each study in which the otoliths were found are presented. The presence of the various invertebrate taxa is indicated.

ITEM	HAWAIIAN WATERS			EASTERN TROPICAL PACIFIC								
	This Study KSN-80-4			Norris & Dohl 1980			Perrin et al. 1973			Fitch & Brownell 1968		
	Total	%	#/%	Total	%	#/%	Total	%	#/%	Total	%	#/%
Family-Genus-Common Name												
Fish	500	100	1/100	Otoliths not available for identification			5668	100	6/100	13839	100	5/100
Myctophidae - Lanternfishes	263	53	1/100				4189	74	6/100	12200	88	5/100
<u>Diogenichthys</u>	0	0	0				3411	60	6/100	1423	10	5/100
<u>Lampanyctus</u>	5	1	1/100				388	7	5/83	2746	20	5/100
<u>Benthosema</u>	0	0	0				281	5	6/100	7606	55	5/100
<u>Myctophum</u>	4	.8	1/100				29	.5	4/67	222	1.6	4/80
<u>Hygophum</u>	27	5.4	1/100				5	.1	4/67	41	.3	4/80
<u>Diaphus</u>	21	4.2	1/100				2	-	1/17	1	-	1/20
<u>Notoscopelus</u>	6	1.2	1/100				0	0	0	0	0	0
<u>Ceratopscepelus</u>	3	.6	1/100				0	0	0	0	0	0
<u>Symbolophorus</u>	0	0	0				5	.1	3/50	16	.1	2/40
<u>Unid. Myctophid</u>	201	40	1/100				68	1	5/83	145	1	3/60
Photichthyidae - Lightfishes												
<u>Vinciguerria</u>	0	0	0				192	3	5/83	1317	10	5/100
Bregmacerotidae - Deep Sea Cod												
<u>Bregmaceros</u>	4	.8	1/100				842	15	4/67	243	1.8	5/100
Melamphidae - Bigscales							424	7	2/33			
<u>Melamphaes</u>	0	0	0				11	.2	1/17	0	0	0
<u>Scopelogadus</u>	0	0	0				413	7	2/33	0	0	0
Bathylagidae - Blacksmelts												
<u>Bathylagus</u>	0	0	0				11	.2	1/17	0	0	0
Scopelarchidae - Pearleyes	3	.6	1/100				5	.1	1/17	0	0	0
Stromateidae - Butterfishes	0	0	0				2	-	1/17	0	0	0
Paralepididae - Barracudinas	0	0	0				1	-	1/17	30	.2	1/20
Unidentified	0	0	0				2	-	2/33	0	0	0
Postlarval Fish												
Apogonidae - Cardinalfish	13	2.6	1/100				0	0	0	0	0	0
Carapidae - Pearlfishes	3	.6	1/100				0	0	0	0	0	0
Holocentridae - Squirrelfishes												
<u>Myripristis - Uu</u>	1	.2	1/100				0	0	0	0	0	0
Bythitidae - Livebearing Brotulas	10	2	1/100				0	0	0	0	0	0
<u>Brotula</u>												
Unknown Larvae												
Pempheris-like - Sweepers	9	1.8	1/100				0	0	0	0	0	0
Cirrhitid-like - Hawkfish	2	.4	1/100				0	0	0	0	0	0
Blenny-like - Blennies	1	.2	1/100				0	0	0	0	0	0
Miscellaneous	187	37	1/100				0	0	0	0	0	0

Table 7 cont. Summary of food items known from Stenella longirostris. For fish, the total number of otoliths collected, the percentage of the total that is comprised by each taxon, the number of dolphins in which each kind of otolith was found, and the percentage of the total number of dolphins examined in each study in which the otoliths were found are presented. The presence of the various invertebrate taxa is indicated.

ITEM	HAWAIIAN WATERS			EASTERN TROPICAL PACIFIC		
	This Study KSN-80-4	Norris & Dohl 1980	Perrin et al. 1973	Fitch & Brownell 1968		
Family-Genus-Common Name	Total % #/%	Total % #/%	Total % #/%	Total % #/%		
Cephalopods	Present but not identified					Present but not identified
Onychoteuthidae						
<u>Onykia</u>			27	4/33		
Ommastrephidae						
<u>Dosidicus</u>			45	3/25		
<u>Symplecoteuthis</u>			14	6/50		
Unidentified			23	1/8.3		
Enoplateuthidae						
<u>Abraliopsis</u>			152	5/42		
Chiroteuthidae			2	1/8.3		
<u>Abralia</u>		46	4/100			
<u>Histioteuthis</u>		1	1/25			
Crustaceans						
Gammarid Amphipod				1/8.3		
Shrimp						
<u>Pasiphaeids</u>		14	2/50			
<u>Sergia</u>		35	2/50			
<u>Acantheephyra</u>		1	1/25			

The fish genera identified from the otoliths are shown in Table 7. This table also includes the results of three other food studies from Hawaiian animals and from the eastern tropical Pacific, for comparison. The fish otoliths from samples collected by Norris and Dohl (1980) were unidentified due to erosion during formaldehyde preservation. Invertebrates were found in the stomach in all four studies, but they were only identified in the work of Norris and Dohl (1980) and Perrin et al (1973).

Lantern fishes (Myctophidae) comprise more than half of the otolith collections. Similarly, Cadenat and Doutre (1959) reported that a large percentage of the otoliths in the stomach of four spinner dolphins collected off West Africa appeared to be myctophids.

In our work most myctophid otoliths were unidentified - below the family level, but Hygophum and Diaphus were the most frequently identified genera. These genera comprised a smaller percentage of the total number of otoliths in the other two studies. Also present in all three samples were specimens of Myctophum and Lampanyctus. The adults of all these myctophids are on the order of 10 - 15 cm long. All are scattering layer fishes found in deep water during the day, and all but Lampanyctus may reach the surface at night. Fitch and Brownell (1968) noted that Lampanyctus does not move above about 200 m depth, even at night.

Bregmaceros, a small (7.5 cm) cod-like fish, was identified in all three studies. This fish reaches the surface at night, but Fitch and Brownell (1968) hypothesized that because of its small size the presence of this species as well as Vinciguerrina and Diogenichthys in the dolphins' stomachs may be due to predation upon the fish by cephalopods then consumed by dolphins. Another consistency between the eastern tropical Pacific collections and Hawaii are unidentified scopolarchids, comprising a small percentage of the total otoliths of our study and that of Perrin et al (1973). Different cephalopods and crustaceans are identified from each area.

All prey items were small (generally less than 20 cm long). While adults of some of the taxa identified in our work may reach 80 cm in total length here they are identified as post larval non-adults of reef fishes that are planktonic in the early stages of life. The 22 April capture date coincides with the peak in recruitment of larval reef fishes in offshore waters. These small prey items are consistent with the mode of feeding suggested by the delicate pincer jaws and many small teeth of spinner dolphins. In sum, the spinner dolphin appears to feed primarily on very small mesopelagic prey.

The consistent presence of Lampanyctus, a deep water form, the presence of only deep water squid, and the absence of epipelagic forms in the samples of Norris and Dohl (1980) suggest that spinner dolphins are feeding at depths of 200 m or below.

The other prey items suggest feeding from 200 m depth or more up to the surface.

Animals taken in the morning had fleshy remains in their stomachs while those obtained in the afternoon did not. This pattern suggests a lack of feeding in the morning and early afternoon (Perrin et al 1973). This correlates well with the observed midday rest period inshore, and the apparent feeding formations seen at night. Further support for this diurnal cycle comes from the frequent observations of defecation within schools entering rest coves in the morning. Often several animals at once could be seen trailing long clouds of fecal material at this time.

Predation

The predation on small cetaceans by sharks has been documented by a number of authors (Arnold 1972, Caldwell, Caldwell and Siebenaler 1965). Norris and Dohl (1980) state:

"Hawaiian spinner dolphins seem to be attacked with some frequency by sharks. Several of the scarred animals we catalogued had obviously been wounded by large sharks. Lunate rows of tooth marks, especially on the flukes and peduncle, some apparently from sharks with a 12 - 15 in. (31-38 cm) gape were noted. This assumed that the scar did not grow with the dolphin, a circumstance we cannot assess. In one case it seemed that the entire tailstock had once been in a shark's mouth. Nicked or tattered dorsal fins may also have been produced by a shark bite."

We can add little to this. Our scars and marks catalogue concentrated on photography of dolphins from above the surface because of this approach produced the most resighting records, and most shark bites are on parts of the body that remain below the surface. One marked animal, Four-nip (#2, an adult male) had the posterior of his fin tattered with what looked like a shark bite.

Discussion

School Structure and the Fishery

When one tries to assess the effects of incidental kill of dolphins in the yellowfin tuna fishery a nagging and unappraised part of the problem has always been the effect upon the integrity of the dolphin school. The question has two parts: first, how much disruption can such societies absorb? And second, is the kill in the fishery likely to affect the immediate integrity of the dolphin school? This study allows an assessment of some

aspects of this broad and complex question.

We have found that spinner dolphin social groupings are remarkably fluid; an individual may move with freedom among many sets of companions and such movements may happen quickly, may take the animal far, and may be reversed. The society in which spinners move seems to depend heavily on learned bonds within groups composed of a great many animals. We feel that the daily caressing bouts, in which partners are changed frequently, may serve to an important degree to reaffirm the bonds necessary for such an extended society based heavily upon learned relationships.

A crucial piece is missing. Does the animal in these peregrinations move totally within the confines of some sort of extended family, or is it more like our own society in which though we spend much time with family we also move within an extended society of friends with no necessary familial relationships? The solution of this puzzle is of consuming theoretical interest, but our present state of knowledge is insufficient to provide a firm answer.

Taking all the incomplete information we can muster into account the model that fits best is the second model; the society composed partly of familial units and more broadly of learned associations far beyond the confines of genetically effective family groups. The pieces are these. Mother-young bonds seem persistent, just as they are known to be in other dolphin societies, especially that of Tursiops (Wells et al 1978, 1980, 1983).

There seem to be associations between individuals that occur, disappear and reoccur over long time spans.

On the other side of the coin dolphin schools seem clearly to be very fluid assemblages that serve as sensory integration systems regardless of their specific composition. The caressing that consumes a considerable fraction of every adult dolphin's day may well be a reaffirmation of relationships in such transitory schools. The school, regardless of its parts, can be a protective system for its constituent animals. Even though fluid with regard to specific members, schools seem to involve a division of essential labor amongst the adult members.

Mating seems to be promiscuous. These features seem beyond the limits of effective kin assemblages, as are the sheer numbers involved. As Connor and Norris (1982) discuss, such a society requires a system of reciprocal altruism in order to function, which may manifest itself not only in the well known cooperative behavior of dolphins, but also in their apparent continual need to reaffirm relationships.

It seems possible that a society such as this, based heavily on widespread learned patterns which are the property of the society, may have more resilience than a more rigid wholly kin-based society. Therefore we expect that dolphin society may well be resilient in the face of the dolphin kill brought on by the tuna industry. We do not expect the essential protective function of dolphin schools to be reduced by the kill.

Population parameters, such as recruitment levels, may become limiting before social disruption does.

What we can say categorically is that the defensive school - the sensory integration system - is built of available animals and the only apparent requirement is that some adults be involved. It may be that some representation from the adult male 'squads' that seem to order the school is also required.

The Integrity of Subgroups

Nearly all workers who have studied dolphin schools have noted their tendency to segregate into recognizable subgroups. These are sometimes grouped according to age and sometimes sex. The tendency toward such segregation seems especially clearly marked in migratory schools where one or more kinds of subgroups may typify a given catch of Stenella spp. (Miyazaki 1977, Kasuya 1972, Kasuya, Miyazaki and Dawbin 1974) and is less evident when resident schools of the eastern tropical Pacific are captured (Perrin, Coe and Zweifel 1976). In Hawaii subgroups are evident within schools but if a whole school was caught it is likely that different age and sex classes would be represented much of the time.

But, even in migratory populations such subgroup segregation is probably a statistical matter (Miyazaki 1977) based on the total geographic spread of a moving population. Only in small samples, geographically speaking, whether of migratory or resident populations, is the subgroup structure apt to be consistently segregated.

The compositional difference between migratory and resident schools is possibly based on three things. First is the tendency in all dolphin schools for certain age and sexual groups to aggregate within the school envelope. Second, the tendency toward fluidity results in high tolerance toward changing inter-mixtures of associates in any large school. And third, when larger schools are migrating, as they do off the Japanese coast where Miyazaki and Kasuya have sampled, their single direction of travel may emphasize the natural tendency toward subgroup aggregation to 'stretch the structure' over a considerable geographic range.

The importance of this is that studies of migratory populations of Stenella attenuata and Stenella coeruleoalba have produced a model of dolphin social structure somewhat different from the patterns we have found with Stenella longirostris schools in Hawaii, or Perrin has found on the yellowfin tuna grounds for either species (Perrin et al 1977). Kasuya, Miyazaki and Dawbin (1974) have postulated that after a neonate Stenella attenuata leaves its mother it joins a juvenile school, and then at adulthood joins a mating school. Miyazaki and Nishiwaki (1978) who studied migratory schools of striped dolphins (Stenella coeruleoalba) in the oikomi fishery of Japan, postulated a similar progression.

Our study suggests that these models may place undue emphasis on the degree of segregation of these subgroups, which may only be far apart during migration, and part of the same school envelope in resident schools.

Comparison of Wild Schools and Those Observed in Tuna Nets

Two sets of observers have studied dolphin behavior underwater in tuna nets. Norris, Stuntz, and Rogers (1977) reported such observations from the dedicated vessel cruise of the seiner Elizabeth C. J., and Pryor and Kang (1978) from a cruise of the Queen Mary. The results of these two studies overlap substantially but differ strongly in some respects. We will attempt to use our knowledge of undisturbed spinner schools as a comparative frame to comment on these differences.

Norris, Stuntz, and Rogers emphasize that dolphins captured in tuna nets were notable for the high level of fear and aggression shown. They noted that it was entirely unnatural for a swimmer to be able to move among such dolphins touching them, and that 'rafting' of dolphins, which consisted of large groups of animals hanging quiescently in the water within the net, was probably related to a closed ring of stimuli from which the animals could not escape. These authors emphasized that from the moment the dolphins were released they fled with great rapidity, as if released from the immobilizing stimuli.

These authors went on to write that when spotted dolphins that had rafted in the open net circle were condensed into a backdown channel they often sank, immobile, often tail first and sometimes piled up on the net below in considerable numbers. It was suggested that this behavior could fit the 'dearousal hypothesis' of Delius (1970), in which an animal in a stressful situation, overloaded with stimuli from all directions, may set in motion patterns that are behaviorally and psychologically associated with sleep. The animal thus disconnects itself from the stimulus overload. This pattern has been suggested as causal in the freezing patterns of birds, snakes and mammals, and in the death-feigning of opossums.

Pryor and Kang, on the other hand, felt that the dolphins they had observed had become so habituated to being netted that they were not experiencing significant levels of fear, but were going about their business in a relatively unstressed way.

Both groups of authors note that learning has occurred in many schools on the tuna grounds. Capture, for a given animal, may be very frequent. Not only are most schools within the eastern and middle part of the Cooperative Yellowfin Regulatory Area (CYRA) markedly more difficult to catch than they were early in the history of the fishery but their behavior in the nets has become increasingly adaptive. Instances in which schools bolt into the net have been reduced, compared to the behavior of naive schools caught for the first time.

Even though Pryor and Kang regard the behavior they observed as relatively normal, their descriptions indicate otherwise. For example, in wild spinner dolphin schools overt aggression is not a frequent pattern. In the nets Pryor and Kang noted extended aggressive interchanges among males, including gaping, snapping (but not biting), striking sideways with the jaws and flukes, threat sounds and gestures, chasing (including, in spinners, the chasing of one male by many others), ramming and group threat displays. Adult and young females were seen gaping at males, and occasionally at their own calves, and making threat sounds and displays, and tooth raking at other adults.

This level of aggression is orders of magnitude more intense than any we observed with undisturbed or captive spinner dolphins. Because we found that aggression was often related to school ordering in normal schools we take this very high level, and the rafting behavior observed in nets, to have a similar function. In the face of stimuli from all directions the dolphins attempt to order the school into a defensive pattern, and aggression is the major means of achieving this.

Pryor and Kang also described rafting, hovering and tail first sinking behavior, all patterns we have never seen at sea. They note six kinds of bubble displays, behavior seldom seen in undisturbed schools (though bubble trails are common and we did see massive bubble release occasionally).

They noted that in agitated animals the white patch on the tip of the rostrum of spotted dolphins sometimes became pink; presumably flushed with blood.

To us, when we compared these descriptions with what we know of undisturbed wild spinner dolphins, they are indications of agitation and stress in the net. In backdown, frequent loss of subgroup structure is a feature also not seen in undisturbed schools, except to some degree during rest. The behavior of dolphins on release from the nets is also instructive. Only when it becomes apparent to them that they are free do they bolt away

from the net and vessel. One moment their behavior is remarkably passive and the next it is active in the extreme, features hardly indicative of normalcy or calmness.

Among seven subgroup types described by Pryor and Kang are 'courting pairs'. The maintenance of courtship in the net would certainly suggest minimal disruption of school activity. But we feel there is no reason to assign only the courtship function to caressing behavior. As we have shown here, this behavior occurs both homo- and heterosexually, and between most age groups. It occurs all year long even though the mating season is circumscribed. There is also no correlation between the incidence of caressing and reproductive hormone level (Wells 1984). We do not regard it as necessarily sexual but instead, outside the mating season, primarily devoted to reaffirmation of relationships, a feature of importance even in a tuna net.

Pryor and Kang have noted what they called "dominant male subgroups", which they could recognize by both sexual features of the animals, and by the resolute, very synchronous swimming they typically showed within the school. We have identified such groups in spinner schools, and have found that they routinely interpose themselves between intruders and the remainder of the school (Figure 1). Pryor and Kang regard them as dominant and report that schoolmates give way to them.

The Acoustic Dimension

Most studies of dolphin sounds recorded in nature have been concerned with the structure of the signals themselves (see Steiner 1980 for a review of the cetacean acoustic behavior literature). Three studies have attempted to analyze suites of sounds in the context of behavior of wild dolphins. Taruski (1976, 1979) classified swimming patterns of North Atlantic pilot whales (Globicephala melaena) and was able to correlate sound emissions with rough behavior classes, even though he was unsure what these classes meant in terms of the daily activity of the whales. Tyack (1976) prepared a more meaningful behavioral classification for South Atlantic bottlenose dolphins (Tursiops truncatus) including some swimming patterns that he felt were concerned with feeding and others with rest. He obtained clear correlations of the frequency of emission of sounds, their types and his behavioral classification.

Ford (1984) has done extensive work on killer whales. He has defined diurnal behavior patterns and their significance to the animals, and he has classified sounds in relation to them. Like our work, he defines classes of recognizable signals (echolocation-type clicks, whistles, and discrete and variable pulsed calls) that occur with variable frequency in relation to behavior class. He assigns to pod-specific calls the function of maintaining the integrity of moving schools where members are

significantly out of visual contact, just as we do whistles in this study. He notes changes in the character of calls in relation to activity level, just as we do here.

His work extends beyond ours by defining with considerable precision the pod and clan specific nature of calls.

The special strength of our work is that more than any study to date we have a secure grasp of the daily activity patterns of the dolphins we studied. We can therefore define the possible function of the sounds we hear in this context. This allows a gross correlation between school behavior and what one might call 'bulk sound emission'. It does not let us arrive at a detailed context specific 'meaning' for given sounds in most cases. We can say firmly what Tyack said tentatively; that certain classes of sound vary strongly in level of occurrence with behavioral state.

Our assignments of functions to these sounds and their variations are much more tentative and hypothetical. While spinner dolphin whistles nicely fit the circumstances under which a dolphin school needs a phatic acoustic system (the open communication channel used, we think, to integrate schools out of visual contact) our supporting data are circumstantial. All we can say at this time is that this assignment brings together both behavior and acoustic emission into an internally consistent scheme.

The most striking correlation we found is between sound emission level and the level of general activity. As the animals become active when they begin to travel, spread out, and feed at night their sounds and their aerial activity both become much more abundant than before. Thus, it seems clear enough that spinner dolphins alternate between behavioral states mediated significantly by vision (especially during rest when vocalization almost ceases) and states mediated largely by sounds.

Leadership

We have demonstrated that the directional movement of spinner dolphin schools is a group process with the basic attributes of a fish school, but added to this reaction system are the memories of experienced, long-lived animals that give the school a "group memory". Direction may be imparted from any point in the school, but usually from behind, to the sides and below undisturbed schools. In times of stress all dolphins in a school may impart direction from any place in the school.

School direction and coordination depend upon the sensory modality in force at the moment.

Because the information on which these group processes is based is diffused through the older age classes of the school it is unlikely that school disruption will result from the death of a single leader.

We suggest, but cannot prove, that the use of islands as rest sites by Hawaiian spinner dolphins and other western Pacific populations of this species (which seems to happen wherever spinner dolphins and islands occur together) is a case of a flexible behavioral response to local geographic conditions and not an indication of great behavioral difference between Hawaiian spinner dolphins and their more oceanic relatives.

The Possible Consequences of Prey Debilitation

If the scheme by Norris and Møhl (1983) that odontocetes may be able to debilitate prey with sound is correct there could be important correlates in spinner dolphin life, and for the tuna-dolphin relationship. Bearing in mind that the method is considered speculative, including by those who proposed it, the following are possible consequences. We present them as frames for thinking and for future data gathering, not as information that is, at this point directly applicable.

If dolphins possess a means of prey debilitation it could be important in the organization of the multispecies aggregations seen on the tuna grounds, which include the tuna, the dolphins, sharks, billfish, small fish and birds. The dolphins could be nuclear, not the tuna as some others have supposed (Au, et al. 1979), because (1) they have means of locating prey that is more powerful than those of other members of such aggregations, and (2) they are able to reduce the escape capability of such prey once it is close by.

Such debilitation should have graded effects, depending upon how close the dolphin is to the prey, and how directly the dolphin is able to ensonify it. This could mean that many prey items escape direct capture by the dolphin and are then more available to the associated species, including tunas, of the multispecies aggregation than they might otherwise be. Acoustic prey debilitation would be expected to be relatively non-specific in its effects, which would enhance such an effect.

Some potential objections to these ideas have occurred to us. We present them with our replies.

(1) The surface-dwelling tuna-dolphin association is localized in the eastern tropical Pacific. If the association is related to prey debilitation why isn't the association found elsewhere?

The shallow thermocline of the eastern tropical Pacific effectively restricts tuna to surface and near-surface waters, while they may stay deeper elsewhere. Dolphins, being tied to the surface as air breathers, cannot form more than very transitory bonds in deep water. In the ETP the lives of all participants tend to be compressed together in the surface water mass.

(2) Why should only certain dolphin species carry tuna if prey debilitation is a root cause, bearing in mind that such debilitation if it exists, is expected to be widespread amongst odontocetes?

For such debilitation to be effective in the tuna-porpoise bond the food items both dolphin and fish eat should be similar. This is the case for spinner and spotted dolphins and yellowfin tuna (Perrin 1973).

(3) Where the thermocline is deep why shouldn't the dolphins and fish swim together at the surface?

There is a cost, perhaps great, for the fish to make great vertical excursions. Perhaps dolphins and fish do continue to associate at depth as dolphins continue to dive to feed, but there seems no reason why the fish should share the dolphins problem of being locked to the surface by swimming repeatedly to the surface if it doesn't have to.

(4) Dolphins sometimes don't appear to lead the tuna-dolphins assemblages. How can they be nuclear?

As we have demonstrated elsewhere in this paper decisions about school direction typically do not come from the leading edge of schools. Also, location of food by the dolphins can be as effective from what appear to be follower positions as from in front. The problem is in the human conception of leadership, not the dolphin's.

(5) If dolphins capture prey by sound they should attract other hangers-on besides tunas.

That could be the genesis of the multispecies aggregations seen.

But the strongest evidence that the dolphin is nuclear in the tuna-dolphin relationship comes from observations from fishermen. They know that to catch dolphins is to catch tuna. The bond of the fish to the dolphins occurs with singular tenacity and no matter what maneuvers the fishermen may make to drive or herd the dolphins the tuna will follow. If the tuna were nuclear it would be expected that encircling or driving the dolphins would merely strip the dolphins from the fish rather than to allow both to be encircled by the net.

We also note that one of us (Norris) has observed spinner dolphins being followed by a single file of small tuna inside a tuna seine. In this case the fish followed the dolphins and not the other way around. Pryor and Kang (1978) noted that in the net dolphins tended to avoid tuna if they could, a feature of the nuclear animal, not its satellite.

Methods

At the start of this study we decided to use several simultaneous approaches to learning about spinner dolphins. Our hope, and our realization, was that this would lead to cross-correlations between methods and a greater understanding than could be achieved otherwise. It seems useful to look back on this design and its individual parts.

The basic cataloguing of individual dolphins and their associates in dolphin schools using photography has been a crucial cornerstone of our work. It allows refined analysis of movements and association beyond the level we have achieved here. It has allowed us to probe into the broadest structure of the society we examined by showing, in aggregate, that our data base continued to grow at a relatively constant rate throughout the study. The society we examined was open rather than closed within the restricted geographic boundaries we set for the work.

The precise positional information provided by theodolite tracking has a similar open-ended aspect. As one learns more and more one's observations develop more precision. By talking behavioral data into tape at the same time positions were being determined behavioral analysis beyond the perceptions of observers was achieved. The details of such matters as traverse length between surfacings, or the precise localization of rest patterns over specific parts of a bay allowed us to make correlations that were otherwise not obvious.

We felt that behavioral observations must involve a means of observing underwater since nearly all of the animal's activities occur there. We felt we needed, somehow, to travel with wild animals in the process. And we needed to record our data with such precision that later analysis could take us beyond our perceptions of the moment. While the focal animal method used by Pryor and Kang (1978) was important, and we used it too, many things happened so fast, and in such profusion, that only by capturing the behavior on film or videotape, and later looking frame by frame could we unravel what actually had happened. Once again the method extended beyond our perceptual capabilities as individual observers. We are far from exploiting underwater observation to its fullest. Our vehicle left much to be desired, even though it served us well. Its design did not let us sex animals

by direct genital examination, except infrequently. Our listening capabilities were limited, and the seaworthiness of the craft limited us to observations deep in rest coves. It was slow and noisy. Videotape, at the time we worked, was of insufficient resolution to allow us to identify individuals, but advances are being made rapidly and it should supplant the more cumbersome filming.

In our underwater work the synchronization between note taking, listening and filming was primitive. Better methods would greatly increase the value of the data we could retrieve.

In our work the availability of captive animals proved an invaluable crosscheck on what we saw more fleetingly at sea. Though captive behavior did involve distortions of natural patterns we usually could come to understand them and to achieve the correlation between captive work and studies in nature. Captive studies allowed a fine-grained analysis of behavior based on knowledge of individuals, their sexes and relationship and reproductive condition not possible at sea. At-sea work provided an overall framework in which to fit captive studies.

We have no illusions about the problem of observer bias in our behavioral observations. Dolphins schools did react to us whether we came as a lone swimmer, or as a recording vessel, in a viewing vehicle, or as a photographer clinging to the bow of an inflatable. Only our observations from our cliffside theodolite station or from shore, truly involved undisturbed animals. This problem provides another reason why such undisturbed observations were so important. By comparisons, we could gauge how much effect we were having.

Another example of probable observer bias comes from our free-swimming work. The swimmer very seldom saw the patterns of deep rest, not we feel because they didn't occur in her area, but because resting animals shied away from her and she tended to let them be.

The swimming method proved to be by no means simple. It requires an intrepid observer because dolphins are sometimes accompanied by sharks, and one with enough endurance to swim with, toward, and after dolphins for long periods. To be maximally effective it required much better recording and filming equipment than we had available to us.

The method of 'announcing presence' by uttering a mimic of a dolphin sound does indeed tend to help a swimmer approach a school. Our swimmer was repeatedly able to enter schools where she seemed to be regarded as relatively innocuous, rather than as a silent threat to be avoided.

But 'dolphin business' is preeminently tied to social relations with other schoolmates. That is, after all, the fabric of

dolphin life. This means that any movement toward a swimmer is apt to be transitory as the school moves by. Dolphins attracted to the swimmer soon leave to catch up with their schoolmates. There is pressure for a dolphin to stay within its school envelope.

Radiotracking proved the only method we had to follow and acoustically record animals at night, and it told us how far dolphins move, and what the process of making a landfall the next morning consists of. It gave crucial insights into gross school movements, showing that not all animals came nearshore to rest every day but some stayed with what we came to regard as the larger population of dolphins offshore.

Aerial surveys allowed us to frame our study in terms of the entire island, rather than in the context of a cove or two. We began to perceive seasonal fluctuations, and relations of dolphin schools to bottom topography.

In short, in order for the difficult task of unraveling dolphin social behavior to be broadly successful it had, itself, to be broadly based. No single method could give us a complete view, and our various vantage points only do part of that task. We still know next to nothing about what dolphins do at night, and about their social arrangements as they dive deeply offshore.

SUMMARY

- (1) The social behavior, population dynamics, acoustics and reproduction of the Hawaiian spinner dolphin, Stenella longirostris, were investigated between May 1979 and June 1981.
- (2) The movements and distribution of spinner schools were investigated using biweekly flights around the shoreline of the Island of Hawaii.
- (3) Intensive studies of the spinner dolphins frequenting Kealake'akua Bay were made from a base camp at the village of Napoopoo. Scans of the bay which described the behavior and the time of arrival and departure of dolphins were made every half hour during daylight hours for the duration of the study.
- (4) A theodolite station set on the face of the Kealake'akua Bay cliff allowed precise tracking of dolphins in the bay.
- (5) Observations of dolphin schools underwater were made from a viewing vessel. It allowed an observer to lie below the water level in a chamber while viewing through a plexiglas bow section.
- (6) A scars-and-marks catalogue was compiled by photography throughout the course of the work. A total of 1233 recognizable dolphins was sighted and 224 individuals were identified.
- (7) The population proved to be open-ended. After an initial flush of new records acquisitions of new animals accumulated at a steady rate throughout the remainder of the study. It is suspected that individuals come and go from a reservoir nearby, perhaps just offshore of the Island of Hawaii.
- (8) The entire population proved to be quite fluid, with association patterns between marked animals changing almost daily. Some relatively stable or recurring subgroups within schools were noted, and many animals appeared to have geographical preferences for certain stretches of coastline. Of 224 identifiable dolphins only 126 were sighted more than once. Thirty-six dolphins were sighted 10 or more times. Using resighting rate a total 'population' from which our marked animals were drawn is calculated at near 1000 animals.
- (9) Modest evidence for a seasonal change in abundance around the Island of Hawaii was obtained suggesting a winter reduction in numbers along the Kona Coast and an increase at other locations.

- (10) Certain specific coves and sandy shorelines were frequented by dolphins while they remained absent from others. The close proximity to an escarpment (100-1000 fathoms) offshore appears to be the determining factor. It is over these deep island slopes that the animals feed at night.
- (11) Specific coves were found to harbor the same general upper number of dolphins throughout the study though the number in residence in each bay at any one time varied greatly. One determining factor appeared to be the areal extent of shallow sandy-bottomed areas over which dolphins could rest during the day.
- (12) Limited tagging and radiotracking was done. It showed that during the night schools traversed more or less parallel to the shoreline, in one case moving back and forth over about 50 km of coastline in 5 days of tracking. The tracks showed that not all dolphins entered shallow bays each day, but many appeared to travel along the shoreline in the nighttime feeding areas.
- (13) One marked animal traveled half way around the Island of Hawaii from the Kona coast to the vicinity of Hilo. This and other tracking data emphasize the fluid nature of the Island of Hawaii population as a whole.
- (14) The diurnal pattern of Hawaiian spinner dolphins was found to be a regular one. Nighttime feeding took place along the island shore, usually between 100 and 1000 fathoms depth. The dolphins moved closer to shore in the hours before daylight when some schools broke away to move inshore to resting coves and sandy open coastline. As this movement takes place the general activity of schools subsides until, once a cove is reached, the dolphins become very slow moving, remaining over specific areas for, on the average 4-8 hours. This pattern we call 'rest'. Almost no aerial activity is evident. Once the rest period is complete, usually in the afternoon, the school abruptly arouses and enters a period of oscillating movements back and forth, either in and out of coves, or back and forth along more open shores. Then, often at dusk, the school moves quickly offshore and abruptly enters spread formation over relatively deep water. Scattered schools assemble into larger feeding aggregations which begin the nighttime traverses along the coastline. Residence in rest coves is much shorter in winter than summer (4 vs about 7 hrs).
- (15) Aerial behavior was classified and studied. Nine more-or-less distinct categories were found; spins, arcuate leaps, tail-over-head leaps, head-slaps, back-slaps, tail-slaps, noseouts, flukeouts, and salmon leaps are described. The abundance of aerial patterns per animal in a school correlates well with its activity level, there being much more

aerial behavior in active than in passive schools. Most patterns seem to produce a sharp slapping sound as the animal reenters, usually from the flukes or fin being slapped against the surface upon reentry. Spins are complex patterns involving a below-the-water precursor behavior and a reentry pattern. Spins seem to have at least two functions; the production of sound and the attempted removal of ectoparasitic remoras.

- (16) Following rest dolphins entered a period of oscillation between active swimming out to sea, and slow return to the resting grounds. This we called "zig-zag swimming". It is thought to involve a social facilitation process during which the 'alertness' of school members is tested prior to moving toward the offshore feeding grounds.
- (17) Once dolphins reach deep water their rapidly traveling schools suddenly disperse widely in what we have termed "spread formation". Its function is unknown, but we speculate that it is related to food finding.
- (18) Acoustic studies correlated the frequency of emission of various classes of sound with behavioral state. Acoustic events were found to cycle regularly between abundant signal emission at night and much depressed emission during the day. All classes of sound were involved. One class, screams, was heard only in the dark (Poe, et al 1935). Almost all sound emission ceased during rest. Sound emission became cyclic during zig-zag swimming, rising in abundance as the animal's activity rose and falling as activity subsided.
- (19) Click trains seemed associated with navigation, feeding and perhaps social behavior while whistles were postulated to be a 'phatic communication system'. Such a system provides an open channel of communication. In this case we suggest that it is used as the means of school integration when vision is ineffective. Since whistles are relatively omnidirectional and stereotyped, and for some species at least, are identifiers of the individual and its emotional state, they provide a means of marking the dimensions of the school for its members in the dark and for transmitting emotionally based information about such things as danger or food sources.
- (20) Burst-pulse signals were felt to carry several kinds of social meaning since they were typically heard during social patterns such as contact, interaction, and aggression.
- (21) The determinants of school shape and the disposition of dolphins within a school envelope are discussed. These include sensory needs of the dolphins, social factors and hydrodynamic constraints.

- (22) Signs and signals used by spinner dolphins are described. These include a variety of pattern and bodily features, and motion such as rolling toward or away from a partner and consequently showing a white belly or a dark back.
- (23) The sensory fields both for sending and reception are discussed for both vision and hearing. Spinner dolphins can see both ahead and behind themselves, and have good lateral fields as well. Both sound transmission and reception are concentrated sharply ahead of the animal.
- (24) Leadership in spinner dolphin schools appears to be a group process lodged in older animals, except during dangerous times when any animal or group of animals can signal through the sensory integration system of the school to provoke turns or other evasive maneuvers.
- (25) Underwater observations were made with the viewing vehicle, by swimming with schools, and by underwater filming and frame-by-frame analysis. Schools were found to contain age and sex based subgroups. Subgroups of young and small juveniles were frequently seen. Subgroups of adult males frequently interposed themselves between observers and the remainder of the school and appeared to carry out protective and ordering functions.
- (26) Mother-young pairs were frequently seen and often had open space within the school envelope. Their interactions are described.
- (27) Rest groups traveled sedately. Resting dolphins swam slightly separated from each other (formation swimming) and with muted subgroup structure.
- (28) Subgroups involving very small young and juveniles were often separated from obvious parents nearby but remained well within the school envelope. Very small young and small juveniles were often paired in these groups.
- (29) In active periods as much as 30% of a school might engage in caressing behavior. This ranged from sedate touching of pectoral fins to group caressing with several animals wriggling in intimate contact. All sexes and age classes were involved, in any combination. During estrus periods mating was noted in such groups, though caressing persisted throughout the year.
- (30) The distinctions between reproductive and social contexts of sexual behavior were examined by comparing behavioral frequencies with reproductive hormone concentrations of captive spinner dolphins. Genital-to-genital contact and mutual ventral presentations occurred most frequently during periods of high male testosterone levels. Beak-to-genital

propulsion may have been related to ovulatory events. All other kinds of contact, one-way ventral presentations and chases occurred with equal frequency regardless of reproductive hormone levels, suggesting a social function for these patterns.

- (31) Observations of captive animals showed behavior to be divided into easily recognizable bouts that extended from a few minutes to about an hour in length. Such bouts were clearly defined events with clear beginnings and oscillations at the end between the existing and the coming pattern. Bouts of echolocation, aerial behavior, caressing and formation swimming were noted.
- (32) Somewhat similar bouts could be discerned at sea, though because of the large numbers of animals in wild schools caressing took on a group character with many and frequent switches of partners.
- (33) Dolphins engaged in click train bouts did so with singleness of purpose and did not direct high intensity sounds at schoolmates.
- (34) Aggressive patterns are described including an S-shaped threat posture that is sometimes accompanied by loud impulsive sound. The posture and its associated movements bear resemblance to the aggressive territorial display of the grey reef shark. The possibility of the dolphin mimicking the shark is discussed.
- (35) The excursion of the spinner dolphin flukes during locomotion is found to reach no deeper than the level of the pectoral fin tips and no higher than just above the base of the dorsal fin. These limits may allow dolphins to swim in close association without hitting one another, and allow a surfacing animal to keep its flukes well below the surface, and therefore avoid serious energy loss.
- (36) Frame-by-frame analysis allowed examination of surface respiration patterns. Dolphins were found to rise to breathe inside a vacuity formed by their own exhalate which blows water away from their partially opened blowhole during earliest exhalation. They were able to complete expiration-inspiration in as little as about 0.5 seconds. The completion of inspiration often took place inside a cavity made by the animal's head as surfacing was completed.
- (37) When schooling fish were introduced into a tank with captive spinner dolphins they were ensonified with rapid high intensity click trains. After more than an hour the fish school became depolarized and the fish seemed in disequilibrium. The possible implications of this are discussed.

- (38) Cycles of the reproductive hormones estrogen, testosterone and progesterone were determined from blood samples taken between September 1979 and October 1980 from captive spinners. A strong concentration peak was found for male testosterone from early spring through later summer. Reproductive cycles for females may involve multiple ovulations during a given spring to fall season.
- (39) The technique of a swimmer approaching and entering dolphin schools is described and discussed. Though demanding of the swimmer it does provide an unusual opportunity for observation.
- (40) Spinner dolphins feed on a variety of mesopelagic prey including crustaceans, cephalopods and fish. Many very small forms are included, and some that do not move above about 200 m depth. Lantern fish are prominent food items.
- (41) Little new information on spinner dolphin predators is presented. Old information of scarring by sharks is reviewed.
- (42) The data from the study are discussed in light of the problem of dolphin kill in the yellowfin tuna industry.
- (43) The applicability of data derived from an insular population of spinner dolphins to problems of open sea populations is discussed. The distinction between such populations was not felt to be important. The island-frequenting habit occurs throughout the range of the spinner dolphin wherever there are adequate islands and is probably related to the food concentrating effect of islands upon mesopelagic life (the Island Effect). A considerable portion of the Hawaiian population seems to live much of the time at sea.
- (44) The extreme fluidity of spinner dolphin social assemblages should minimize the effects upon the larger society of the dolphin kill on the tuna grounds.
- (45) The protective function of schools seems to operate regardless of the composition of the school, perhaps for long as an adult cadre of animals is present.
- (46) The differing population structure for Stenella schools reported from the Japanese coast compared to that in the eastern tropical Pacific is discussed. The differences are felt due to the fact that one population (Japan) is migratory while the eastern tropical Pacific animals are more-or-less resident.
- (47) Evidence is given to support the idea that dolphin schools in tuna nets are in an extremely stressful environment that may even induce dearousal and result in sinking of netted

animals.

- (48) Adult male subgroups which have been described from dolphin schools caught in tuna nets are described for Hawaiian spinners and seem to have a protective, or ordering function in the school. They often interpose themselves between observers and their school.
- (49) The tuna-dolphin bond is discussed. It seems clear that the dolphins are nuclear and that the tuna follow as part of a multispecies aggregation.

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